

**NEST SITE SELECTION BY COMMON EIDERS: RELATIONSHIPS WITH
HABITAT FEATURES, MICROCLIMATE AND INCUBATION SUCCESS**

A Thesis

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By

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ABSTRACT

Habitat selection theory presumes that organisms are not distributed randomly in their environments because of habitat-specific differences in reproductive success and survival; unfortunately, many previous studies were either unable or failed to look for evidence of processes shaping nest site selection patterns. Furthermore, little is known about adaptive nest site selection in northern environments where habitats often have little vegetation and time and climatic constraints may be pronounced. Therefore, I investigated patterns of nest site selection by common eider ducks (*Somateria mollissima*) at an island colony in Canada's Eastern Arctic, and looked for evidence of selective processes underlying these patterns by employing experimental and observational techniques.

I characterized physical features of (a) non-nest sites (b) active nest sites and (c) unoccupied nest sites that had been used in previous years. Habitat features that distinguished non-nest sites from unoccupied nest sites were also important in distinguishing between active and unoccupied nest sites during the breeding season. Active nest sites were closer to herring gull (*Larus argentatus*) nests, farther from the ocean and had organic substrates. In general, habitat features associated with nest use were not strongly associated with success after the onset of incubation. Nests near fresh water ponds were more successful in one study year, but in the other two study years successful nests were initiated earlier and more synchronously than were unsuccessful nests. Common eiders settled to nest first near the geographic centre of the colony, whereas sites near the largest fresh water pond were occupied later; distance to ocean had no observable effect on timing of nesting. Nest density was greater farther from the ocean, but timing of nest establishment did not differ between high and low density plots.

I tested whether moss or duck down placed in nest bowls could increase nest establishment, or advance laying date. I placed this extraneous material in bowls before nesting and found no difference in likelihood of nest establishment; however, bowls containing duck down were initiated earlier (or had higher survival) than those containing no nesting material. To investigate the role of nest shelter and microclimate in nest site choices and female body condition, I placed plywood nest shelters over established nests. Temperature probes indicated that artificially-sheltered females experienced more moderate thermal environments and maintained higher body weight during late incubation than did unsheltered females. However, few eiders nested at naturally-sheltered sites, possibly because nest concealment increases susceptibility to mammalian predators. My results suggest that eider nest choices likely reflect trade-offs among selective pressures that involve the local predator community, egg concealment, nest microclimate and energy use.

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DEDICATION

For my Grandparents

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Theory suggests that variation in animal reproductive success and survival can lead to non-random patterns of habitat use, and many studies have shown positive correlations between habitat use and fitness (Martin 1988a, Robertson 1995, Munday 2001, Kolbe and Janzen 2002). Studies of avian habitat selection have played an important role in shaping current understanding of adaptive habitat use, and nest site choice is a commonly studied aspect of avian habitat selection (Jones 2001). If some nest sites are better than others (i.e., increase an individual's fitness), relative use of those sites could be favored. To better understand patterns of avian nest site use, and selective processes and trade-offs that may underlie these patterns, I studied the breeding ecology of female common eider ducks (*Somateria mollissima*; hereafter "eider") in the Canadian Arctic. Most studies of avian nest site use are conducted in regions with greater habitat heterogeneity than those in the Arctic (i.e., greater topographic relief, more complex and/or dense vegetative cover). I investigated patterns of eider nest site selection using both experimental and observational techniques, thus furthering our understanding of selective factors that could influence nest site choices and breeding success among birds.

1.2 Study Site

Work was conducted on Mitivik Island (64°02'N, 81°47'W), a small (~0.23 km²), low-lying (< 8 m elevation) nesting colony located in East Bay, Southampton Island, Nunavut (Figure 1.1). The island had numerous patches of low-lying tundra vegetation, granite rocks,

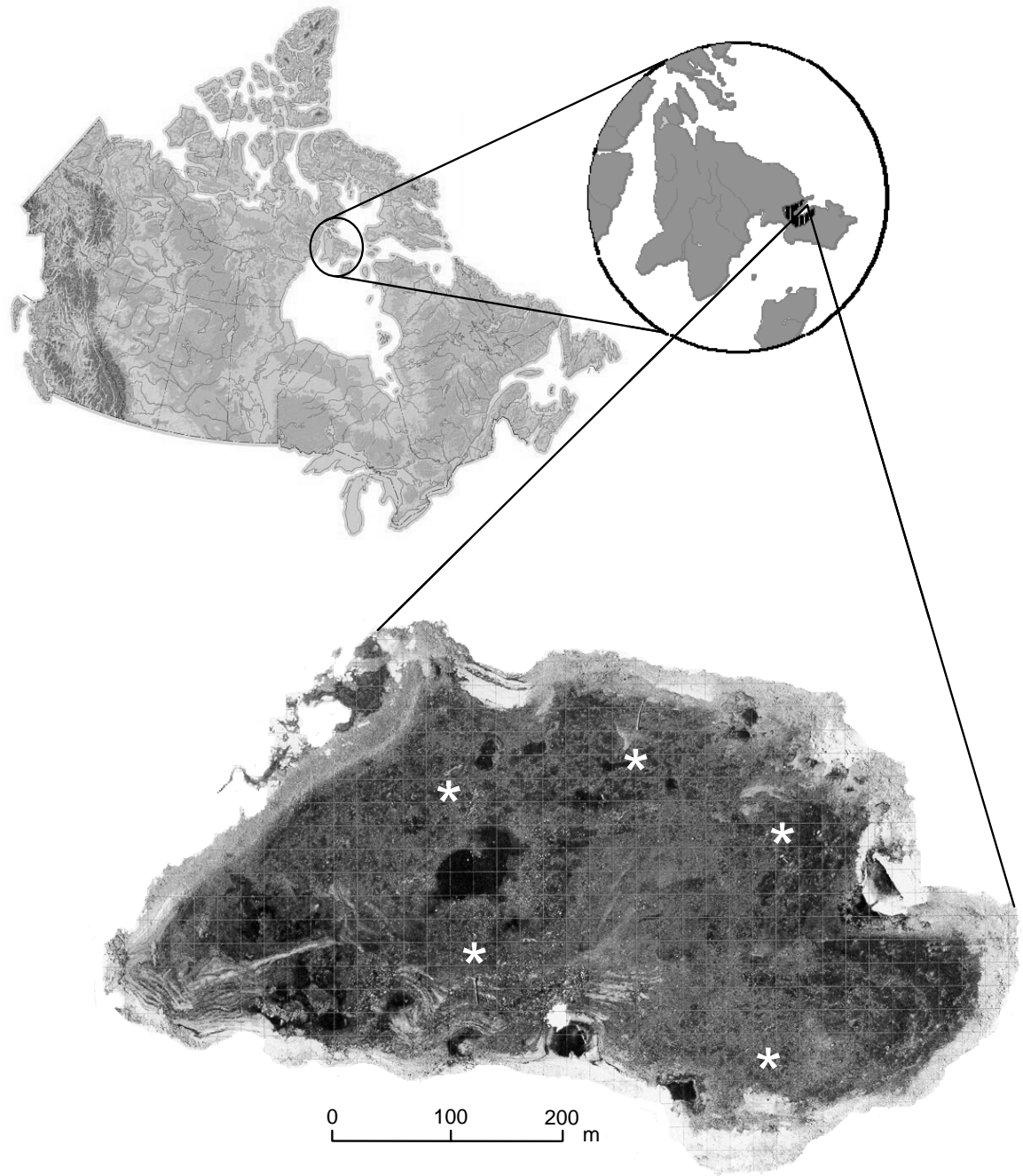


Figure 1.1. Mitivik Island is located within East Bay Migratory Bird Sanctuary (black & white bars), approximately 4 km offshore of Southampton Island (within circle), Nunavut, Canada. Asterisks (*) indicate locations of long-term study plots on island airphoto (image of Canada used with permission of Natural Resources Canada 6-3-2006).

and several small (< 0.5 ha) fresh water ponds, some of which dried out as summer progressed if they were not replenished with precipitation. Mitivik Island lies just south of the Arctic Circle, experiences almost continuous daylight during the nesting season, and can attract ~4500 eider, 40 king eider (*S. spectabilis*), 30 herring gull (*Larus argentatus*), 400 black guillemot (*Cepphus grylle*), 20 snow bunting (*Plectrophenax nivalis*), 10 Canada goose (*Branta canadensis*) and 5 brant goose (*B. bernicula*) pairs (Allard and Gilchrist 2002). This island supports one of the largest known nesting concentrations of eiders in the Canadian Arctic (Abraham and Ankney 1986). Eiders typically arrive in mid-June, nest in late June/early July, and few remain beyond mid-August. A small cabin and tents are present in the region of lowest eider nesting density.

1.3 Study Species

Eiders are colonial-nesting sea ducks with a northern circumpolar distribution. Adults feed on benthic marine macroinvertebrates, and generally remain within maritime and marine coastal regions throughout the year. Eiders are seasonally monogamous, and pairing is thought to occur in the late winter or early spring. Breeding habitats vary greatly, ranging from southerly forested regions in Maine and eastern Scotland, to Svalbard, Norway, and Canada's high Arctic (Bourget 1970, Milne 1974, Prach et al. 1986, Bustnes et al. 2002). Arctic-nesting eiders are considered extreme capital breeders, and therefore depend almost exclusively on resources acquired before reproduction to meet energetic costs of egg production and incubation (Korschgen 1977, Bottitta 2001); consequently they undergo degenerative physiological and anatomical change while incubating (Korschgen 1977).

Eiders nest on the ground, typically in shallow depressions which they line with down feathers (hereafter “nest bowls”). In the Canadian Arctic, most nests are established in pre-existing nest bowls, while a few females construct their own (e.g., on sand beaches). In many northern locations, nest bowls are well established and could reflect hundreds of years of occupation (Cooch 1965, Jonsson 2001). The Mitivik Island colony has existing nest bowls that are re-used in different years and are easily identified before arrival by nesting females. Shortly after hatch, hens and ducklings leave the island colony for brood-rearing sites along the coasts of nearby Southampton Island (≥ 4 km away).

Up to seven subspecies of common eider are recognized which differ slightly in colour and size (Goudie et al. 2000). The eiders nesting at Mitivik Island are primarily northern (*Somateria mollissima borealis*) and Hudson Bay (*S. m. sedentaria*) subspecies, although western Arctic (*S. m. v-nigrum*) and Atlantic (*S. m. dresseri*) individuals have also been rarely observed.

1.4 Objectives and Organization of Thesis

My work was conducted as a component of a larger ecological study initiated in 1996. Complementary aspects of the larger project include investigations of eider survival, toxicology, behavioural ecology, and predator-prey interactions. My overall goal was to investigate patterns of eider nest site use in a natural selection context. In Chapter 2, I describe patterns of eider nest site use, paying particular attention to comparisons of used nest bowls, available unused nest bowls, and non-nest sites. I then investigate associations between nest attributes and nest loss during incubation. In Chapter 3, I discuss colony-wide patterns of nest settlement, and results of an experimental study to investigate the influence of

extraneous nest material on nest bowl use. An appendix presents results of an experimental study on the effects of nest shelters on late-incubation body weight of females and incubation microclimate. In Chapter 4, I discuss current understandings of relationships between habitat use and natural selection. In particular, I explore proximate mechanisms through which natural selection could cause subsequent adaptation of habitat preferences and lead to non-random habitat selection patterns.

CHAPTER 2: PATTERNS OF COMMON EIDER NEST SITE SELECTION ON MITIVIK ISLAND, NUNAVUT

2.1 Introduction

Many studies of avian habitat selection are entirely descriptive, and fail to frame discussions in a natural selection or evolutionary context (Clark and Shutler 1999, Jones 2001). Uniform and random animal distribution patterns are rare in nature, and non-random distribution patterns likely are shaped by diverse and often simultaneous selective forces. Because avian nest site choice has presumably evolved in relation to predation, local availability of resources and microclimate, consideration should be given to these factors (and possibly others) when investigating habitat selection patterns.

Here, I examine patterns of nest site selection and incubation success by Arctic-nesting eiders, and discuss results in light of current understanding about processes that affect choice of nest site (i.e., potential for natural selection). Eiders nest across a wide range of habitats, but little is known about biogeography of nesting Arctic eiders. Eiders nesting in southern regions frequently select nest sites with overhead vegetative cover (Bourget 1970, Milne and Reed 1974, Freemark 1977, Bolduc et al. 2005), but many northern breeding sites lack vegetation sufficiently tall to conceal nests (Cooch 1965, Prach et al. 1986). Studies of nest site choice often discuss the role of nest concealment in site selection and fate (Martin 1988b, 1996, Traylor et al. 2004, Bolduc et al. 2005), but less is known about nest site selection in regions with little or no vegetative cover. Therefore, I examined what features were associated with eider nesting at a northern breeding colony. Available nesting habitats on my study site appear superficially similar; the island has low relief with granite boulders and gravel interspersed with patches of moss, low-lying vascular plants and numerous freshwater

ponds. I evaluated nest site selection by comparing habitat features of successful nests, depredated nests, previously-used nest bowls and non-nest sites. I predicted that nests would be distributed non-randomly, and would occur on organic substrates and be situated near fresh water and other eider nests. If ongoing selective processes shape habitat preferences, then site features that distinguish between nests and non-nest sites could also be those that best distinguish between successful and unsuccessful nests. Timing of breeding is an important component of breeding success in northern birds (e.g., Lepage et al. 2000, Martin and Wiebe 2004), so I also included it in my evaluation. I predicted that late-nesting individuals may be more prone to nest failure because these may be poor quality birds that are more susceptible to nest loss via abandonment or predation.

2.2 Methods

2.2.1 Observation Blinds, Study Plots and Nest Monitoring

Five long-term study plots were established in 1998 to monitor nesting across the range of nest densities observed within the colony (Figure 1.1). To minimize disturbance and allow observation within regions of higher nesting density, plywood observation blinds adjacent to plots were accessed through canvas A-frame tunnels (15-100 m long), with openings at the colony periphery where nesting density was low. Plywood blinds (1.2 x 1.2 x 1.2 m) had 3 removable rectangular openings (20 x 80 cm) for observation using spotting scopes and binoculars. Eiders have nested successfully within 5 m of blinds. Plots varied in size (1039 to 6950 m²), and collectively encompassed ~7% of the island. Blinds not associated with long-term plots were also present for behavioural research, and to aid in detection of nasal-tagged and banded individuals.

In this study, data were collected from late May to mid-August 2000-2002. Four of five long-term study plots were monitored in 2002. Following spring arrival of eiders, human activity within nesting regions of the colony was rare and, in many cases, the need to reduce human disturbance for observational studies limited data collection in specific areas. Additionally, eider nest density was high and nest visitation caused flushing of many females and subsequent aggregations of avian predators (primarily herring gulls and parasitic jaegers, *Stercorarius parasiticus*). For these reasons, clutch size was unknown for nests within study plots and leg bands of incubating females were rarely observed due to high incubation constancy (Bottitta et al. 2003).

All observable nest bowls within each study plot were monitored from blinds twice daily (morning and evening; generally ≥ 8 hours between checks) throughout nesting and eider presence was recorded. Eider hens lay one egg per day and incubation starts after the second or third egg is laid (Cooch 1965, Swennen et al. 1993). When eiders commence incubation, they no longer leave the colony to feed and incubation constancy is very high (99.8%; Bottitta et al. 2003). Nest bowls were recorded as being used (i.e., females laid clutch and commenced incubation) if a female was observed on the bowl for 3 consecutive observations. Nest bowls that did not meet these criteria were unused, or failed during laying or very early incubation.

Incubation onset was the date when an eider hen began to consistently remain sitting on the nest bowl (i.e., for two consecutive observations; often continuously thereafter). Female attendance was recorded for the duration of incubation. Nests were successful if hatch was confirmed by observing ducklings within nests, or incubation was tracked for 22 days or more and egg membranes were present after hatch (Schmutz et al. 1983, Götmark and

Åhlund 1988). A nest was classified as failed if predation was observed, if incubation lasted fewer than 22 days, or if bloody egg remnants were found in the nest. I was generally unable to distinguish between abandoned nests and those lost to predators. Nest success was classified as unknown if incubation lasted more than 22 days, but no ducklings were observed and no membranes were found when nest site characteristics were measured. Because I was unable to document nest loss during egg laying, I use the term “incubation success” instead of “nest success” for clarity.

2.2.2 Nest Site Characterization

Bowls in which nests were established were characterized after hatch (2000-2002). The following variables were chosen to reflect the potential significance of nest predation, local availability of resources, and nest microclimate (Gloutney and Clark 1997) based on (a) findings of other studies and/or (b) potential biological significance at the study site.

Distance to nearest herring gull nest: Eiders nest sympatrically with herring gulls on the study island. Herring gulls did not force incubating hens off of their eggs but preyed upon nests during egg-laying, took eggs most often singly from unattended clutches during eider incubation breaks, or preyed upon ducklings during departure from the colony (K. Allard, in prep.). Despite predation, herring gulls may also increase eider nest success by excluding other predators (Götmark and Åhlund 1988, but see Kellett et al. 2003). In all years, initiation of herring gull clutches occurred before onset of common eider egg-laying.

Distance to fresh water pond: Time away from nest may increase susceptibility to egg cooling, nest disruption or predation. Females take short incubation breaks (generally < 15 min) and generally fly or run to drink freshwater from ponds on the island (Bottitta 2001, Bottitta et al. 2003). Eiders often drink at fresh water ponds visible from their nests and will

return to defend their nests when predators approach (Bottitta 2001). Furthermore, Schmutz et al. (1983; see also Robertson 1995) found the highest nesting densities of eiders in La Pérouse Bay near relatively large areas of open water which appeared to facilitate landing and taking flight.

Distance to ocean: Herring gulls nesting on the study island hold all-purpose breeding/feeding territories which they defend against con- and heterospecifics (K. Allard, in prep.). However, territories are larger at the periphery of the island (i.e., near the ocean), and non-territorial gulls and other avian predators (e.g., parasitic jaegers) may be better able to intrude gull territories and “steal” eider eggs in areas near the ocean.

Distance to eider nest: Having a close neighbor(s) may aid in protection and warning, and allow eiders to spend more time sleeping (Criscuolo et al. 2001). Furthermore, eiders at this colony are known to nest near their relatives (McKinnon et al. 2006), providing an explanatory mechanism for group defense behaviour.

Nest bowl substrate (rock/gravel versus organic): Although gravel is present in many regions of the island, organic substrates have lower thermal conductance and may provide insulative benefits to nesting eiders and eggs. Loose organic substrates (i.e., loose moss or peat within bowls) may also help to conceal eggs from predators during laying when eggs are often left unattended (see Chapter 3). Several categories of nest substrate were measured but were collapsed into 2 categories for analyses: organic (primarily moss or peat), and inorganic or “rocky” (primarily rock or gravel).

Habitat adjacent to nest: Habitat structure (e.g., vegetation, rock) may confer microclimatic advantages and influence nest site choice (Hardy and Morrison 2001, Hoekman et al. 2002, Hartman and Oring 2003; see also Kilpi and Lindström 1997), but these

relationships remain poorly understood (Kim and Monaghan 2005). Mitivik Island lacks tall vegetation, but rock structure might influence nest concealment and microclimate. Habitat type within a one m radius of the bowl was recorded, and sites were classified as organic or rocky (as above).

Nest bowl sampling was intensified in 2001, and all nest bowls within all plots were characterized. In many northern locations, nest bowls are well established and could reflect hundreds of years of occupation (Cooch 1965, Jonsson 2001); this allowed me to document characteristics of bowls where nests had not been successfully established in 2001, but had been used previously. Observers were unable to track all nests within plots due to limited visibility in some regions, so I also characterized all bowls that had nests established in them but could not be reliably tracked. It was occasionally unclear whether depressions in the ground were nest bowls; depressions were only characterized as bowls if they appeared to have been used as nests previously, and eggshell was present in them (eggshells remain within bowls between years; P. Fast, pers. obs). I also characterized non-nest sites (see Jones 2001), sampled systematically (Krebs 1999). Within each plot, I placed ropes (knotted at 10 m intervals) to sample potential nest sites at 10 m grid intervals. To ensure consistency, I was present for all nest bowl measurements in 2001 (some distance measurements were recorded by other observers). Additional characteristics sampled at all sites in 2001 only are described below:

Local bowl density: Number of nest bowls within 3 meter radius of the focal nest or site. As above, neighbors (including relatives) may aid in protection and warning.

Distance to nearest nest bowl: As above, eiders may select sites adjacent to others and gain protection.

Nest bowl rim (rock/gravel versus organic): The periphery of the nest bowl may also affect nest insulation. However, it should be noted that eiders may not be selecting organic rims; rather, organic rims may be present because eiders have selected those nest sites, fertilized them through defecation and enhanced vegetation growth.

Large adjacent rocks: My study site lacks vegetative nest cover, but eiders may nest adjacent to rocks, possibly to gain shelter from weather (Goudie et al. 2000; see also Appendix). To document occurrence of rocks adjacent to nest bowls, one end of a one m stick was placed in the center of the nest bowl, oriented 45° above horizontal, and rotated through 360°. Rock structure was considered present if rock obstructed this rotation within each of 8, 45° sectors. For example, rock was recorded as being present to the north if stick movement was obstructed by rock between 337.5° and 22.5°.

Distance to fresh water pond at hatch: Some fresh water ponds dry up as the season progresses if not replenished by rain. Because gulls remain present and prey upon unattended eider eggs throughout incubation, greater distances to fresh water in late incubation may increase susceptibility to egg loss due to increased time required by nesting eiders to travel to water during incubation breaks.

The island is almost free of snow during egg-laying, so snow cover was not considered as a factor in nest site selection. Because eiders leave the colony with their ducklings for brood-rearing areas on Southampton Island several km away, proximity of nest location to brood rearing sites was also not evaluated. Furthermore, eiders forego feeding during incubation (Tinbergen 1958, Korschgen 1977, Goudie et al. 2000) and are not known to feed at the study island (Bottitta 2001); therefore, proximity to food source was not evaluated. Vegetation changes through time were also not considered because island vegetation appears

to change little within the nesting period, or between years. Finally, overhead rock cover was also measured at nest sites because concealment correlates with nest success in other ground-nesting ducks (Guyn and Clark 1997, Traylor et al. 2004). However, very few sites had overhead rock cover and this variable was excluded from analyses (see Appendix for results and further discussion).

2.2.3 Data Analysis

Statistical analyses were performed with SAS (SAS Institute 1990). Data collected in 2001 included all available nest bowls (used & unused) and non-nest sites within plots. Before proceeding with discriminant function analyses (DFA), principal component analysis (PROC PRINCOMP; SAS Institute 1990) was used to test for multicollinearity among variables (Hair et al. 1998). In 4 analyses restricted to 2001 data, 10 variables were of interest; the first principal component explained between 24.5-28.0% of the variation, lower than expected by chance alone (29.2%, broken stick model; Jackson 1993, Shaw 2003). Eight variables were of interest in 3 analyses using data 2000-2002; the first principal component explained between 21.6-28.0% of the variation, also lower than expected by chance alone (33.9%). Therefore, I used original variables in all subsequent analyses.

DFA (PROC DISCRIM, SAS Institute 1990) was used to discriminate among groups based on physical characteristics. Several nest site variables were not normally distributed (PROC UNIVARIATE, SAS Institute 1990), so transformations (log, square root, arcsine, tangent) were conducted to improve normality where appropriate. Differences between within-group covariance matrices were tested using chi-square tests of homogeneity and quadratic DFA was performed when group covariances were heterogeneous (Williams 1983, SAS Institute 1990). Plot sizes were unequal (i.e., unbalanced design); however, initial

analyses showed little difference in DFA comparisons if larger plots were removed, so all plots were included in analyses. DFA was used to discriminate among 3 groups (used bowls, unused bowls, and non-nest sites) simultaneously using site attributes. Two-group DFAs were then used to determine (1) how available habitat differs from nest habitat by comparing nest bowls (i.e., used and unused nests combined) and non-nest sites, (2) differences between used and unused nest bowls and (3) differences between successful and unsuccessful nests in 2001. I did not obtain complete measurements in several cases, so sample size varied among analyses.

DFA was also used to compare successful and unsuccessful nests using variables collected in all 3 years. These models included date of incubation onset, and date of incubation onset relative to annual median onset (i.e., “synchrony” index; absolute value). These variables (a) could not be included in analyses evaluating non-nest or unused sites and (b) allowed me to assess the importance of a female characteristic simultaneously with nest bowl variables (Bolduc et al. 2005). Up to 75% of available bowls within a plot can be used in one season; because I was unable to track bowls between years (despite attempts to mark them individually) many of the same bowls were inevitably re-measured in consecutive years. Therefore, years were analyzed separately to avoid pseudoreplication, and to investigate differences among years.

Because successful eider nests at the study site may hatch up to 6 eggs and eggs are often lost singly (K. Allard in prep.), a binary measure of incubation success (i.e., failed versus successful) may give incomplete information. Ordinal logistic regression (PROC LOGISTIC, SAS 1990; proportion odds model, Hosmer 2000) was used to evaluate relationships between nest characteristics and number of successfully hatched eggs (2000-

2002; estimated as number of ducklings observed within hatched nests, or number of membranes in nest post-hatch). Few nests successfully hatched 5 ($n = 14$) or 6 ($n = 1$) ducklings and were included in a single category (hatched ≥ 4). To meet assumptions of proportional odds criteria (SAS 1990, χ^2 , $P > 0.05$), I limited analyses to 5 physical site characteristics.

2.3 Results

In 2001, all nest bowls ($n = 794$) within plots were characterized; 379 bowls were either unused or failed during laying or early incubation, and 401 had common eider nests successfully initiated (additionally, 1 brant goose, 2 Canada geese, and 6 king eiders also nested within plots but these nests were excluded from analysis). Only bowls which could be tracked and had established nests were sampled in 2000 ($n = 122$) and 2002 ($n = 235$). Some bowls could not be observed from blinds, had two nests successfully initiated within one breeding season, or use could not be determined; these were excluded from analyses where appropriate. In addition, nests were excluded if observers were unable to determine success, if observers may have caused failure, or nests were used for experiments. Non-nest sites ($n = 217$) were also systematically sampled within plots in 2001.

Initial DFA used site characteristics to discriminate between nest bowls used by eiders ($n = 395$), nest bowls unused by eiders (or in which a nest was not successfully established; $n = 373$), and non-nest sites ($n = 179$) in 2001. These 3 groups were clearly distinguishable from one another (Wilks' Lambda = 0.65, $df = 18$, $P < 0.0001$; Fig. 2.1), and DFA correctly classified 59.3% of sites (36.4% better than chance; Titus et al. 1984). Non-nest sites tended

to be closer to the ocean than nest bowls, whereas nest bowls tended to have higher local nest bowl density and were generally closer to herring gull nests.

Summary statistics (Table 2.1) and 2-group DFAs (Table 2.2) were used to further compare groups. Nest bowls ($n = 783$) differed significantly from non-nest sites ($n = 179$), and were more likely to have organic substrates, be farther from the ocean, and have a higher density of nest bowls within 3 m (Wilks' Lambda = 0.81, $df = 10$, $P < 0.0001$; Tables 2.1, 2.2). Used nest bowls ($n = 396$) also differed significantly from unused bowls ($n = 373$), and were more likely to be near active herring gull nests and in regions of higher local bowl density (Wilks' Lambda = 0.81, $df = 10$, $P < 0.0001$; Tables 2.1, 2.2). Successful ($n = 329$) and unsuccessful ($n = 26$) nests in 2001 were also compared using the full variable set, and the overall discrimination was insignificant (Wilks' Lambda = 0.95, $df = 10$, $P = 0.124$; Table 2.2).

DFA was also used to compare successful and unsuccessful nests in 2000-2002 using variables collected in all 3 years (except distance to fresh water pond at hatch, which was not measured in 2000). In 2000 (20 unsuccessful nests, 88 successful nests), nests near fresh water ponds were more likely to be successful (Wilks' Lambda = 0.85, $n = 108$, $df = 8$, $P = 0.0424$; Table 2.3). In 2001 (14 unsuccessful nests, 276 successful nests), nests where females began incubating near median incubation onset date were more likely to be successful (Wilks' Lambda = 0.91, $n = 290$, $df = 9$, $P = 0.0026$; Table 2.3). In 2002 (22 unsuccessful nests, 153 successful nests), nests with earlier incubation onset were more likely to be successful (Wilks' Lambda = 0.88, $n = 175$, $df = 9$, $p = 0.0092$; Table 2.3). Ordinal logistic regression was used to evaluate relationships between physical site characteristics and number of successfully hatched eggs. Only one of 3 models was significant; nests established closer

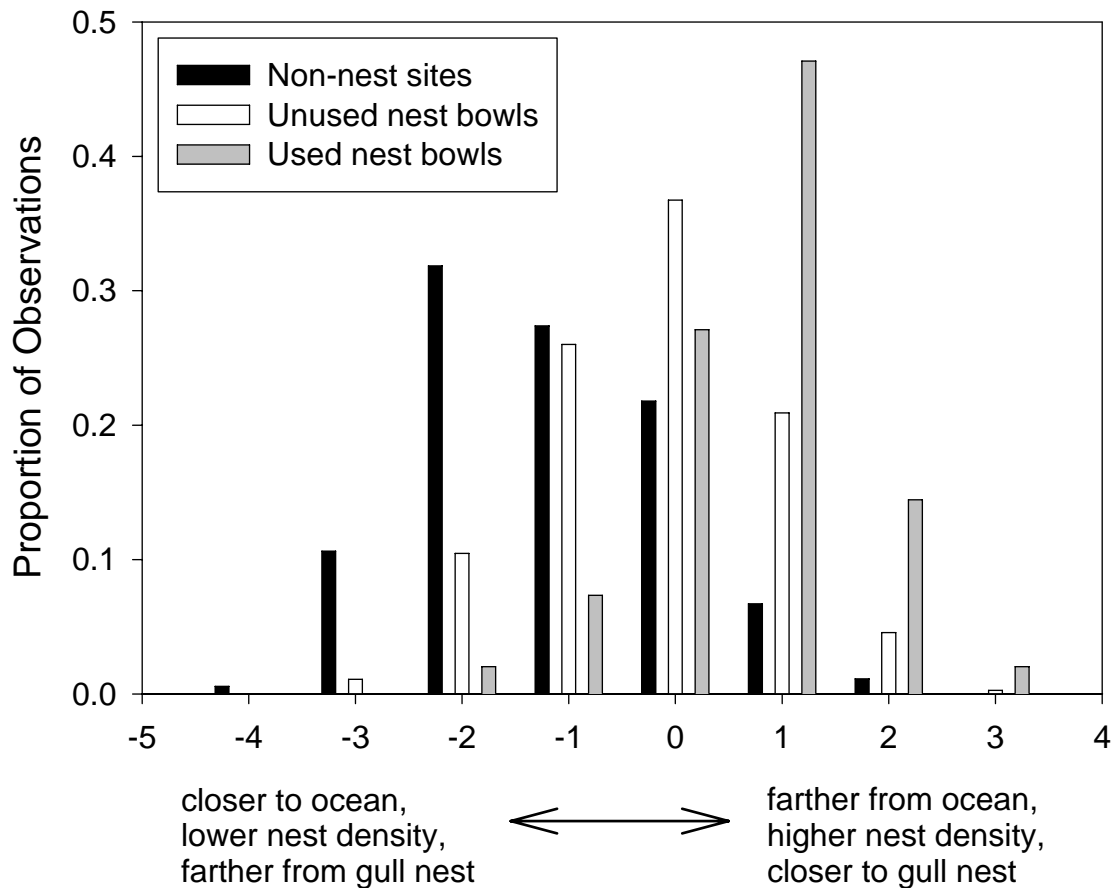


Figure 2.1. Distribution of discriminant function scores for non-nest sites ($n = 179$), unused nest bowls ($n = 373$), and nest bowls used by common eiders (*Somateria mollissima*; $n = 395$) on Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada, in summer 2001. Non-nest sites (black bars) were more likely than used nest bowls (gray bars) to be closer to the ocean, have lower local nest density, and be farther from gull nests; unused bowls (white bars) had intermediate characteristics. The multivariate habitat gradient (x-axis) ranged from sites close to the ocean, farther from gull nests and with low common eider nest density (left, negative values) to sites nearer the centre of the island, closer to gull nests and with higher nest densities (right, positive values).

Table 2.1. Means (± 1 SD) for variables measured at systematically-selected non-nest sites, available but unused nest bowls, and nest bowls with successfully initiated common eider (*Somateria mollissima*) nests. Percentage occurrence of organic substrate and presence/absence of large rocks adjacent to bowls/sites are also shown for each sample group. Data were collected summer 2001 on Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada.

Site variable	Non-nest sites (n = 215)	Unused bowls (n = 377)	Used bowls (n = 398)
Distance to nearest herring gull nest (m)	76.2 \pm 29.8	71.6 \pm 29.3	57.5 \pm 26.4
Distance to fresh water pond during nest initiation (m)	26.0 \pm 19.0	25.2 \pm 20.1	28.8 \pm 16.9
Distance to fresh water pond during nest hatch (m)	67.6 \pm 24.2	71.0 \pm 23.9	62.4 \pm 22.9
Distance to ocean (m)	74.7 \pm 24.5*	82.8 \pm 20.1	93.4 \pm 21.0
Distance to nearest nest bowl (m)	5.1 \pm 4.1	4.3 \pm 3.9	2.8 \pm 2.6
Number of nest bowls available within 3 m	1.3 \pm 1.6	1.9 \pm 1.8	2.7 \pm 2.0
Organic substrate at nest bowl/site (% occurrence)	40%	69%	87%
Organic substrate of nest bowl rim or 15 cm site radius (% occurrence)	23%	31%	35%
Organic substrate within 1 meter of nest bowl/site (% occurrence)	16%	14%	6%
One or more large rocks adjacent to nest bowl/site (% occurrence)	24%	39%	46%

*n = 183

Table 2.2. Discriminant function coefficients for models discriminating between non-nest sites, unused nest bowls, and nest bowls used by common eiders (*Somateria mollissima*) at Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada in summer 2001. Shown for each variable is the canonical coefficient for models discriminating between (a) systematically sampled non-nest sites & all available nest bowls (b) nest bowls used & unused by eiders (c) successful & unsuccessful nests. Larger absolute values of coefficients imply that the variable has a stronger influence in discriminating between groups. Negative values suggest nest bowls, used nest bowls or successful nests were more likely to be closer to feature of interest⁽¹⁻⁵⁾ and were more likely to have rocky substrate⁽⁹⁾. Positive values suggest these sites had more nest bowls available nearby⁽⁶⁾, were more likely to have organic substrate⁽⁷⁻⁸⁾ and have one or more large rocks adjacent to nests⁽¹⁰⁾.

Site variable	All nest bowls vs. non-nest sites ^a	Used vs. unused nest bowls ^b	Successful vs. unsuccessful ^c
¹ Distance to nearest herring gull nest	-0.343	-0.580	0.139
² Distance to fresh water pond during nest initiation	-0.056	0.300	-0.271
³ Distance to fresh water pond during nest hatch	0.143	-0.389	0.227
⁴ Distance to ocean	0.506	0.543	0.340
⁵ Distance to nearest nest bowl	-0.342	-0.156	0.125
⁶ Number of nest bowls available within 3 meters	0.423	0.439	-0.007
⁷ Nest bowl / site (rocky/organic)	0.682	0.467	0.695
⁸ Nest bowl rim or w/in 15 cm of site (rocky/organic)	0.122	0.084	-0.107
⁹ Substrate w/in 1 meter of nest bowl / site (rocky/organic)	-0.192	-0.260	-0.119
¹⁰ One or more large rocks adjacent to nest	0.304	0.156	0.096
Percent correct classification	84.3	66.7	91.5
Percent improvement on chance discrimination (\pm 95% C.I.)	50.0 \pm 7.5	33.0 \pm 6.8	32.4 \pm 23.6
Significance of overall discrimination	<0.0001	<0.0001	0.124

^a coefficients with loadings > |0.150| are significant; in bold (P < 0.05, two-tailed)

^b coefficients with loadings > |0.105| are significant; in bold (P < 0.05, two-tailed)

^c coefficients with loadings > |0.374| are significant; in bold (P < 0.05, two-tailed)

Note: sample sizes are given in text

Table 2.3. Discriminant function coefficients for models discriminating between successful and unsuccessful nests used by common eiders (*Somateria mollissima*) at Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada, 2000-2002. Larger absolute values of coefficients imply that the variable has a stronger influence in discriminating between groups. Negative values suggest successful nests were more likely to be closer to feature of interest⁽¹⁻⁵⁾, were more likely to have rocky substrate⁽⁶⁻⁷⁾, timed nesting earlier than the median incubation onset date⁽⁸⁾, or timed nesting synchronously with the median incubation onset date⁽⁹⁾.

Site variable	Successful vs. Unsuccessful nests		
	2000 ^a	2001 ^b	2002 ^c
¹ Distance to nearest herring gull nest	-0.276	0.313	0.075
² Distance to fresh water pond at nest initiation	-0.848	-0.240	0.075
³ Distance to fresh water pond at nest hatch	-----	0.065	0.202
⁴ Distance to ocean	-0.081	0.079	0.287
⁵ Distance to nearest common eider nest	-0.074	0.129	0.136
⁶ Nest bowl / site (rocky/organic)	-0.072	0.351	0.065
⁷ Substrate w/in 1 meter of nest bowl / site (rocky/organic)	-0.020	-0.040	-0.182
⁸ Timing of nesting	0.207	-0.483	-0.720
⁹ Synchronous timing of nesting	0.109	-0.640	-0.325
Percent correct classification	87.0	96.6	86.9
Percent improvement on chance discrimination (\pm 95% C.I.)	53.4 \pm 23.2	64.9 \pm 21.8	33.8 \pm 25.7
Significance of overall discrimination	0.0424	0.0026	0.0092

^a coefficients with loadings $> |0.423|$ are significant; in bold ($P < 0.05$, two-tailed)

^b coefficients with loadings $> |0.497|$ are significant; in bold ($P < 0.05$, two-tailed)

^c coefficients with loadings $> |0.404|$ are significant; in bold ($P < 0.05$, two-tailed)

Note: sample sizes are given in text

to fresh water ponds were more likely to hatch more eggs in 2000 (Table 2.4).

Given relationships between distance to fresh water pond at nest initiation, as well as between nesting synchrony with incubation success in 2000 and 2001, respectively (Table 2.3), I tested for a putative adaptive response in the subsequent year (Clark and Shutler 1999). Linear regression was used to evaluate the relationship between incubation onset date and distance to fresh water pond at nest initiation ($n = 293$, $r^2 = 0.001$, $p = 0.59$) and at hatch ($n = 293$, $r^2 = 0.05$, $P < 0.0001$). In 2001, nests were likely to be successful if they were initiated during peak egg-laying, but in 2002 nesting was not more synchronous (2000, 3 July \pm 5.5 SD, $n = 111$; 2001, 25 June \pm 4.5 SD, $n = 293$; 2002, 4 July \pm 5.2 SD, $n = 229$).

2.4 Discussion

I found strong evidence of nest site selection in eiders (Table 2.1). Active nests were closer to herring gull nests, farther from the ocean, and were more likely to have organic substrates than non-nest sites. However, no consistent linkages between pattern and process were evident across study years. This could have occurred for several reasons. First, I was unable to document nest loss during egg laying (see methods), and egg loss could be related to nest features during this period. Eider nests are poorly attended during laying (Goudie et al. 2000), and certain nest types may have been chosen to reduce egg loss risks during that period (see Chapter 3). Second, although habitat choices may reflect ongoing selective pressures, I would suggest they may also reflect innate habitat preferences that are vestiges of selective forces experienced earlier, but which no longer play a role in fitness and for which there are no current costs (or insufficient time has passed for their loss). Lastly, given the annual variation I observed, certain pressures may have fitness significance in some years but not

Table 2.4. Ordinal logistic models showing relationships between ordinal measure of nest success (hatched one egg, 2 eggs, ... ≥ 4 eggs) and nest site variables of common eiders (*Somateria mollissima*). Data were collected on Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada, 2000-2002.

Site variable	<u>2000</u>		<u>2001</u>		<u>2002</u>	
	χ^2	P	χ^2	P	χ^2	P
Distance to nearest herring gull nest	2.08	0.15	0.61	0.43	2.94	0.09
Distance to fresh water pond at initiation	13.82	0.002	0.01	0.93	0.05	0.82
Distance to fresh water pond at nest hatch	-----	-----	0.42	0.23	0.004	0.95
Distance to ocean	0.02	0.89	0.54	0.46	1.73	0.19
Distance to nearest common eider nest	0.46	0.50	0.26	0.61	0.04	0.84
Nest bowl / site (rocky/organic)	0.04	0.84	0.38	0.54	0.11	0.74
<u>Whole model</u>						
Wald χ^2	16.6		5.31		8.10	
df	5		6		6	
N	88		320		157	
P	0.005		0.51		0.23	

others. Habitat selection is a process that operates at the level of individual organisms, and population level selection patterns result from a summation of responses of individuals with varied experiences (Wiens 1985). Habitat use patterns may reflect optimal responses to differential fitness among habitats (thereby including responses to resource availability, competition, and predation), but environmental variability within and between years may change fitness associated with certain habitat types (see Wiens 1985, Clark and Shutler 1999).

2.4.1 Inter-annual Variation

Different variables were associated with likelihood of incubation success in each study year, and this pattern has generally been observed in other years. Studies began on the island in 1996, and several years were defined largely by individual events; in 1997, polar bears (*Ursus maritimus*) swam to the island and caused catastrophic egg loss through direct predation; in 2005, 200 dead eiders were found on the colony and all 21 sent for testing were confirmed to have died from avian cholera (*Pasteurella multocida*; H.G. Gilchrist, pers. comm.). Proportion of successful nests varied between years: 73.0% (89/122) in 2000, 89.4% (344/385) in 2001, and 82.1% (193/235). During 2000-2002, no “catastrophic” nest failures were documented. An examination of nest failure dates showed that in all 3 study years, there were only two occasions when more than 4 nest failures occurred on a single day, and on one of these occasions failures were likely caused by investigator activity (observations excluded from analyses; see Methods).

In 2000, nests established near wetlands had a higher chance of success (average distance to wetland at initiation was $28\text{ m} \pm 16\text{ SD}$ successful vs. $48\text{ m} \pm 19\text{ SD}$ failed). Gulls are more likely to leave the island during low tide, presumably to access food resources in the intertidal zone (K. Allard, in prep.). Ice break up within East Bay was also the latest in the 3

study years (2000-July 9, 2001-June 24, 2002-July 8), and gulls were more likely to forage on the colony than in 2001 (K. Allard, in prep.). If predation pressure was higher in 2000 (for example, due to scarcity of alternative, non-eider food sources for gulls), proximity to fresh water ponds may have played a role in egg loss susceptibility. Females with nests located farther from fresh water ponds may have spent longer periods away from their nests on brief drink breaks, increasing susceptibility to egg loss (Bottitta 2001; see also Cooch 1965, Bolduc et al. 2005). I was unable to measure clutch size in this study, but Bolduc et al. (2005) found eider nests with large clutch sizes and early laying dates were associated with poorly concealed nest sites that were close to the shorelines of St. Lawrence River islands.

In 2001 and 2002, the best predictors of incubation success were relative timing of nesting (Table 2.3). Timing of nesting is likely important for Arctic-nesting birds in general given short breeding seasons (Martin and Wiebe 2004) and should be based on several reliable cues, especially in single-brooded species (Svensson 1995) such as eiders. The relationship between timing of nesting and nest success in greater snow geese (*Anser caerulescens atlanticus*, a single-brood species) also varies between years, favoring early nesters in some years, synchronous nesting in others, and showing little pattern in others years (Lepage et al. 2000). Number of young geese surviving to the first winter was also very low among late-nesting birds, with early-nesters also showing a slight decline; unfortunately, little is known about how timing of breeding might influence survival to fledging and subsequent recruitment in eiders.

Herring gulls may increase eider nest success by excluding other predators (Götmark and Åhlund 1988), but the placement of nests near gull nests may be a result of shared habitat preferences (Kellett et al. 2003). At my study colony, between 30 and 40% of eider eggs laid

may be depredated by gulls in some years, and about 75% of eggs were observed to be taken singly (K. Allard, pers. comm.). Most eggs are taken during laying, when eiders do not defend their nests and gulls have easy access to prey. Nesting in synchrony with other eiders on the colony may reduce risk of egg loss because more eggs become available than gulls are capable of consuming (Sovada et al. 2001). Relatively few eider eggs are taken once their incubation commences, and gulls appear to exploit other food resources later in the season (K. Allard, in prep.). In 2001, eider nests established nearest to median clutch initiation date had higher chances of incubation success (Table 2.3). During early laying in 2001, numerous early-season nest failures were also likely attributable to periodic visits of arctic fox (*Alopex lagopus*) before ice break-up (see Sovada et al. 2001). The visits may have been by the same fox, that was observed flushing hens from nests and cacheing their eggs on several occasions over the course of about one week. In 2002, no arctic fox was observed on the island during eider egg-laying. Early-nesting eiders in 2002 may have had higher incubation success because they were higher quality individuals; unfortunately, habitat quality and individual quality are often confounded in correlative studies because high quality individuals may nest first and obtain better nest sites (Kim and Monaghan 2005). This may also be true of eiders; females with high body reserves have been found to lay larger clutches and nest relatively early (Spurr and Milne 1976, Yoccoz et al. 2002, Hanssen et al. 2003a, Hanssen et al. 2004). Bolduc et al. (2005) concluded that eiders rely principally on attendance to protect nests because nest success was only marginally related to nest site characteristics such as nest concealment. The observation that late-nesting individuals in 2001 and 2002 had higher probability of nest failure (Table 2.3) is consistent with these observations, as is the importance of timing of nesting at my study site.

At the study colony, eiders had choices between available nest bowls in all years. However, laying was synchronous (Bottitta 2001, this study) and, if high quality nesting sites are limited, individuals may select higher quality nests in an ideal despotic or pre-emptive manner (Fretwell 1972, Dias 1996; see also Freemark 1977, Robertson 1995). Female eiders generally show high fidelity to breeding areas but not nest sites (Goudie et al. 2000), and data from the study colony are similar (H.G. Gilchrist, unpublished). Furthermore, if numerous bowls of similar quality are available, there may be little benefit for a female to select a bowl she has used previously, and it may be more advantageous to nest at high densities or in relation to kin (McKinnon et al. 2006).

2.4.2 Nesting Strategies

Inter-annual variation in pressures, that appear to have occurred at my study site (Table 2.3), could favor flexible nesting strategies among individuals across years. Eiders are long-lived sea ducks (Goudie et al. 2000), and individuals would therefore have opportunities to adapt strategies based on genetic or learned information (see discussion Chapter 4). Adapting behavioural strategies presumed to be based on learning have been documented in birds (Danchin et al. 2004), largely through studies of breeding dispersal (e.g., Jackson et al. 1989, Powell and Frasch 2000). Given that other behaviours with genetic bases are circumstance-specific (e.g., migration and control of its timing), genetic templates of habitat choice could presumably be adjusted depending upon circumstance. I was unable to detect broad patterns of adaptive responses, and the capacity of eiders to adapt nesting strategies between years remains poorly understood.

McKinnon et al. (2006) reported that female kin groups at the study site may arrive together and that kinship is a factor in nest site selection. They evaluated genetic relatedness

of nesting females to nearest neighbors (that had nested slightly earlier) and found that female associations were not random and aggregations of female eiders were often composed of related individuals during nesting. Furthermore, 5 of 13 focal females had one or more full sibling-equivalent relationships as one of their three nearest neighbors. These eiders may subsequently benefit from communication and detection of predators such as herring gulls, arctic fox, parasitic jaegers and polar bears (Criscuolo et al. 2001), as well as group defense against herring gulls. Given that eiders can nest in family groupings, perhaps they choose the highest quality nesting region available at time of arrival (McKinnon et al. 2006). Although female eiders “prospect” for potential nest sites with males (Goudie et al. 2000), the type of bowl females selected was not influenced by males (McKay 2004). Some benefits of nest site choice may also accrue after nest site departure. For example, some sites may offer improved access to fresh water (DeVink et al. 2005) or brood-rearing sites.

2.4.3 Energy Conservation and Nest Microclimate

Because eiders rely on stored reserves throughout incubation, energy conservation may have shaped evolution of their nest site choices and incubation behaviours (see Korschgen 1977, Criscuolo et al. 2001, Hanssen et al. 2003a). As in other waterfowl species (Mallory and Weatherhead 1993, Blums et al. 1997), eider nest abandonment is thought to be condition-dependent (Tinbergen 1958, Korschgen 1977), although Bottitta (2001) found eiders whose nests failed at the study site had higher predicted late-incubation body weight than those that successfully hatched (~300 g difference). Bottitta (2001) also found that, among females for which incubation was experimentally extended, those that abandoned their nests had higher predicted late incubation body weight than those that hatched. However, experience was a confounding factor and could not be sampled. Poor body condition may

also lower eider nest success (Bottitta et al. 2003, Hanssen et al. 2003b), increase likelihood of duckling abandonment (Bustnes and Erikstad 1991, Bustnes et al. 2002, Hanssen et al. 2003c), and decrease likelihood of breeding in subsequent years (Yoccoz et al. 2002). I was unable to distinguish between abandoned and depredated nests (as in other studies; see Maddox and Weatherhead 2006), but eider nest abandonment can be a significant cause of nest failure (Korschgen 1977, Bourgeon et al. 2006).

Both incubation behaviour (Criscuolo et al. 2001) and nest microclimate are likely important determinants of eider energy expenditure (Kilpi and Lindström 1997). Local habitat features can influence nest microclimate (see Appendix), and energy loss by thermal conductivity could also influence incubation energetics (White and Kinney 1974, McCracken et al. 1997). I found that nest bowls used by eiders were more likely to have organic substrates than either unused nest bowls or non-nest sites. Eiders may have selected such sites for insulative benefits and/or these sites may have organic substrates because eiders have been consistently selecting them for other reasons and fertilizing the local area with feces.

2.5 Conclusions

Physical features of nests were generally poor predictors of incubation success compared with timing of nesting at my study site. Females may reduce predation risk by nesting synchronously and in proximity to conspecifics. Selecting bowls with organic substrates could aid in egg concealment (see Chapter 3) and reduce energy loss (see Appendix). Access to fresh water was a correlate of success in 2000, but eiders weren't found to strongly select sites adjacent to fresh water ponds. Although costs and benefits of using habitats with certain characteristics may vary spatially or temporally, habitat choices

influenced by natural selection could reflect long-term optima (Clark and Shutler 1999). Different biotic and abiotic factors appeared to influence eider incubation success on Mitivik Island; given variations between study years, I suggest eiders are likely facing ongoing refinements of nesting strategies in response to selection. Results from this study suggest that physical characteristics of nest sites may have some influence on eider nest success, although our results are consistent with Bolduc et al. (2005), who suggested that eiders rely principally on nest attendance to protect their nests. Further study into relationships between individual quality, site choice, and breeding success would aid our understanding of adaptive habitat use.

CHAPTER 3: NEST CONTENTS AND COLONY-WIDE SETTLEMENT PATTERNS

3.1 Introduction

Avoiding detection by predators is one way that ground-nesting birds increase their fitness. Although waterfowl often nest conspicuously in Arctic colonies (e.g., McCracken et al. 1997, Goudie et al. 2000), incubation constancy is typically high and eggs are often only available to small and mid-size predators when nest attendance is interrupted. Concealment may aid in preventing egg losses during nest absences by hindering detection by predators (Lancaster 1964, Greenquist 1982). Observational research conducted on the study colony has determined that eider eggs are most susceptible to predation during laying (K. Allard, pers. comm.) when nests are attended intermittently by eider hens (Goudie et al. 2000).

Goudie et al. (2000) suggested that female eiders churn up old material within a nest bowl before laying to permit air circulation and drying of the nest bowl, but I suggest this material could also serve an additional egg concealment function. Although most nest bowls at the colony contain little extraneous material immediately before nesting (presumably due to storms which remove the previous year's nesting material), eider hens have frequently been observed adding loose materials, such as moss, to line nest bowls during the laying period (P. Fast, pers. obs), possibly to conceal eggs. Eiders may also preferentially choose bowls with evidence of previous use or success, which could include old body down or loose vegetation within bowls. Therefore, I evaluated this hypothesis by testing the predictions that eiders may: a) preferentially choose sites containing cues of previous use or success; and, b) prefer and/or be more successful at initiating nests in bowls that contain materials to conceal eggs because this decreases predation risk during laying. Because eiders could add concealing materials such as moss or down to desirable nest bowls, I predicted further that addition of

nesting material would not increase likelihood of nest initiation. However, desirable nest bowls already containing extraneous material would be immediately available to hens for egg concealment; therefore, I predicted that nests containing nest materials would be used first. Due to synchronous nesting by Arctic eiders, addition of down to nests was unlikely to be interpreted as within-season failure. Rather, it might be an indicator of previous use, presumably enhancing attractiveness of down-filled nests.

Second, I describe colony-wide patterns of nest initiation. Nest density varied among five long-term study plots, but variation in density and timing of nesting within other regions of the colony was poorly understood. Evidence from other seabirds (Hipfner 1997, Wendeln 1997, Morbey and Ydenberg 2000, Arnold et al. 2004) and anatids (Lepage et al. 2000, Blums and Clark 2004) suggests that timing of breeding may be related to parental quality, and that late-nesting birds breed less successfully than those nesting early. Furthermore, nesting densities are often uneven within avian breeding colonies, possibly reflecting differences in nest site quality (microclimate, predation risk; e.g., Gaston et al. 2002). High quality nesting regions may be limited, and individuals may select higher quality nests, producing nesting patterns that match distributions expected under ideal despotic or pre-emptive models (Dias 1996). Nesting near colony edges may increase risk of nest loss (e.g., Gaston et al. 2002), and individuals of poorer quality may be relegated to these areas (Coulson 1968). Therefore, in 2003, I evaluated differences in timing of nesting and nest density to describe colony-wide settlement patterns in relation to habitat features on Mitivik Island.

3.2 Methods

3.2.1 Egg Concealment During Laying

I experimentally manipulated 90 nest bowls before nesting in 2003. All loose nest materials were removed from nest bowls under observation (i.e., dead vegetation, egg membranes, down), and bowls were randomly assigned to one of three treatments: (1) feather down added (one liter, uncompressed) (2) moss added (one liter, uncompressed) (3) nothing added; bowl remained empty. Experimentally-placed moss was obtained before the 2003 nesting season from wetland fringes and broken into $\sim 8\text{cm}^2$ pieces; down (frozen over two winters to kill ectoparasites) was obtained from the colony following hatch in 2001, and egg shells and membranes were removed by hand. I moistened each 1L parcel of down and moss with 250 mL of water (obtained from a wetland on the island) to prevent it from being blown away after placement, and to simulate materials available in and adjacent to unmanipulated bowls. One liter of nesting material represents approximately the maximum amount that would be available in unmanipulated nest bowls immediately prior to nesting. Nests were manipulated on 18 June 2003, with a brief visit to each nest bowl on 22 June to ensure that feather down and moss were still in nest bowls.

Following manipulation, nests were observed daily (21 June - 10 July) from observation blinds to document the likelihood of occupation and timing of nest initiation within individual nest bowls. To avoid misclassification of non-nests as nests, my criterion for a successful nest initiation was three consecutive observations of a hen sitting on a specific nest cup. Time constraints prevented establishment of unmanipulated control nests within experimental plots, so mean nest initiation date of unmanipulated bowls was estimated using

observations from the nearest long-term study plot. Differences in timing of nest initiation were examined using one-way ANOVA (PROC ANOVA, SAS Institute 1990).

3.2.2 Colony-Wide Settlement Patterns

I monitored 21 plots (each 20 x 20 m) from 6 blinds daily during nest initiation (23 June – 15 July 2003). I was unable to observe some areas of the colony due to local topography, so plots were selected based on visibility from blinds and to provide representative sites throughout the colony. I monitored each plot throughout nest initiation to evaluate differences in timing of nesting and nest density between different regions of the colony. During daily nest observations, I recorded number of females that appeared to be sitting on nests within each of the 21 plots.

Differences in timing of nesting and nest densities were evaluated in relation to three physiographic features thought to be of potential biological significance. Distance to the closest edge of the largest fresh water pond on the island was evaluated because eiders often nest near water, and large water bodies may facilitate take-off and landing (Schmutz et al. 1983). Distances to ocean (high tide line) and geographic centre of the island were also measured because nesting success may be higher at central locations within colonies, and poor quality individuals may be relegated to sites on the margins of the colony (Coulson 1968, Gaston et al. 2002).

To evaluate timing of nesting between groups (e.g., near versus far from ocean), proportions of nests established over the initiation period were compared using Kolmogorov-Smirnov two-sample tests. For these 2-group comparisons, plots were assigned to categories evenly (e.g., half assigned ‘nearest ocean’ and half assigned ‘farthest from ocean’). Relationships between nest density and plot location were investigated using regression. For

high density plots, I developed logistic growth curves (Hoehler 1995) to estimate number of established nests within each plot (estimated as asymptote; PROC NLIN, SAS Institute 1990). Plots with few established nests (< 5) violated model convergence criteria, so nest density was estimated from raw data.

3.3 Results

3.3.1 Egg Concealment During Laying

A total of 69 nests was successfully initiated (measured by onset of incubation) in 90 experimental nest bowls; 25 nests were initiated in bowls with down, 24 in bowls with moss, and 20 where nesting material had been removed. No difference in likelihood of successful initiation was detected among groups ($\chi^2 = 2.61$, $df = 2$, $P = 0.27$), however there was a difference in timing of nest initiation among treatments (one-way ANOVA; $F_{df=3,124} = 6.21$, $P = 0.019$). Nest bowls containing down had earlier incubation onset than unmanipulated bowls (Figure 3.1; Tukey test, $df = 124$, $k = 4$, $P < 0.001$). Because incubation onset dates from unmanipulated bowls were estimated from a long-term study plot in an adjacent region of the colony, differences in timing of initiation between treatment groups were also evaluated separately using one-way ANOVA ($F_{df=2,66} = 4.19$, $P = 0.019$). Bowls containing experimentally-placed down had earlier incubation onset than bowls containing no nesting material (Figure 3.1; Tukey test, $df = 66$, $k = 3$, $P = 0.014$). On average, hens successfully initiating in bowls containing down began incubating 2.6 days before hens in nests lacking added materials.

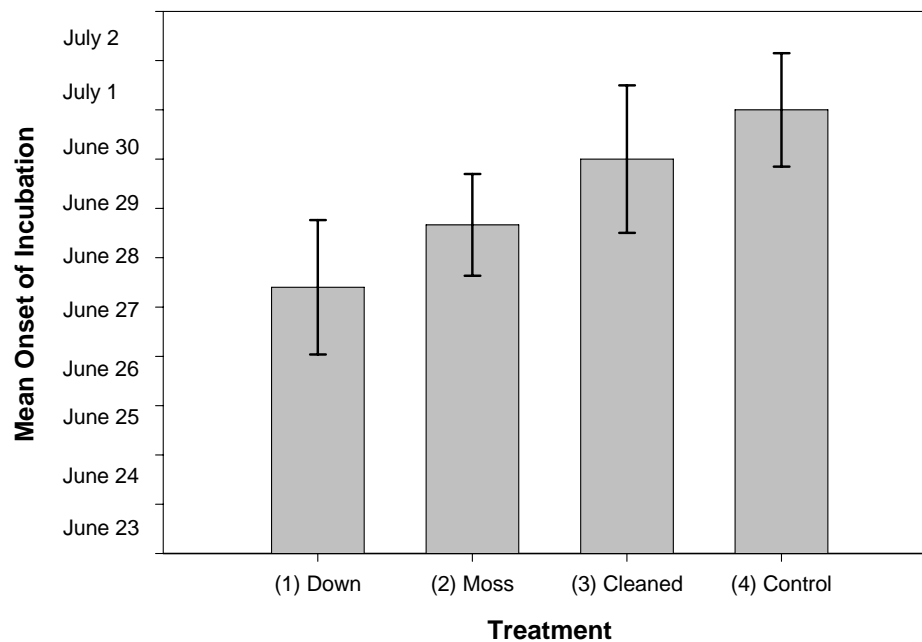


Figure 3.1. Mean dates (\pm 95% CI) of incubation onset for common eider (*Somateria mollissima*) females on Mitivik Island, Nunavut, Canada in June and July 2003. Nest bowls were randomly assigned to three experimental treatments before nest initiation: (1) containing down (2) containing moss, (3) cleaned of nesting material ($n = 25, 24, 20$, respectively). Estimates of unmanipulated control nests (4) were obtained from adjacent non-experimental plot ($n = 59$).

3.3.2 Colony-Wide Settlement Patterns

In 2003, no eiders successfully initiated nests in 2 of 21 study plots, and these were excluded from analyses when appropriate. Plots nearest the colony centre had a higher proportion of earlier incubated eider nests than did plots located on the periphery (K-S Test, two sample: $D_{MAX} = 0.059$, $n_{near} = 1728$, $n_{far} = 1632$, $P = 0.006$), while plots closer to the main pond had a lower proportion of earlier incubated eider nests than did plots farther from main pond (K-S Test, two sample: $D_{MAX} = 0.068$, $n_{near} = 1921$, $n_{far} = 1439$, $P = 0.001$). There was no difference in timing of nest incubation onset between plots closer to or farther from the ocean (K-S Test, two sample: $D_{MAX} = 0.040$, $n_{near} = 1531$, $n_{far} = 1829$, $P = 0.13$).

No difference was found in timing of nest establishment between low (≤ 8 nests established; 9 plots) and high (≥ 9 nests; 10 plots) density plots (K-S Test, two sample: $D_{MAX} = 0.039$, $n_{low} = 650$, $n_{high} = 2710$, $P = 0.40$; Figure 3.2). Nest density was not correlated with distance to colony centre or distance to the main pond (linear regression; $n = 21$, $r^2 = 0.12$, $P = 0.13$ and $n = 21$, $r^2 = 0.13$, $P = 0.11$, respectively). Nest density was somewhat higher in plots located farther from the ocean (linear regression; $n = 21$, $r^2 = 0.18$, $P = 0.056$).

3.4 Discussion

I studied relationships between nest use, timing of nesting and nest features at very different scales. At the scale of nest sites, presence of duck down in nest bowls resulted in an earlier onset of incubation but neither down nor moss produced higher nest bowl use relative to controls. At the scale of the colony, nests were established earlier near the geographic centre of the island, whereas sites near the largest wetland were occupied later. Nest density increased in areas farther from the ocean, but timing of successful nest establishment did not

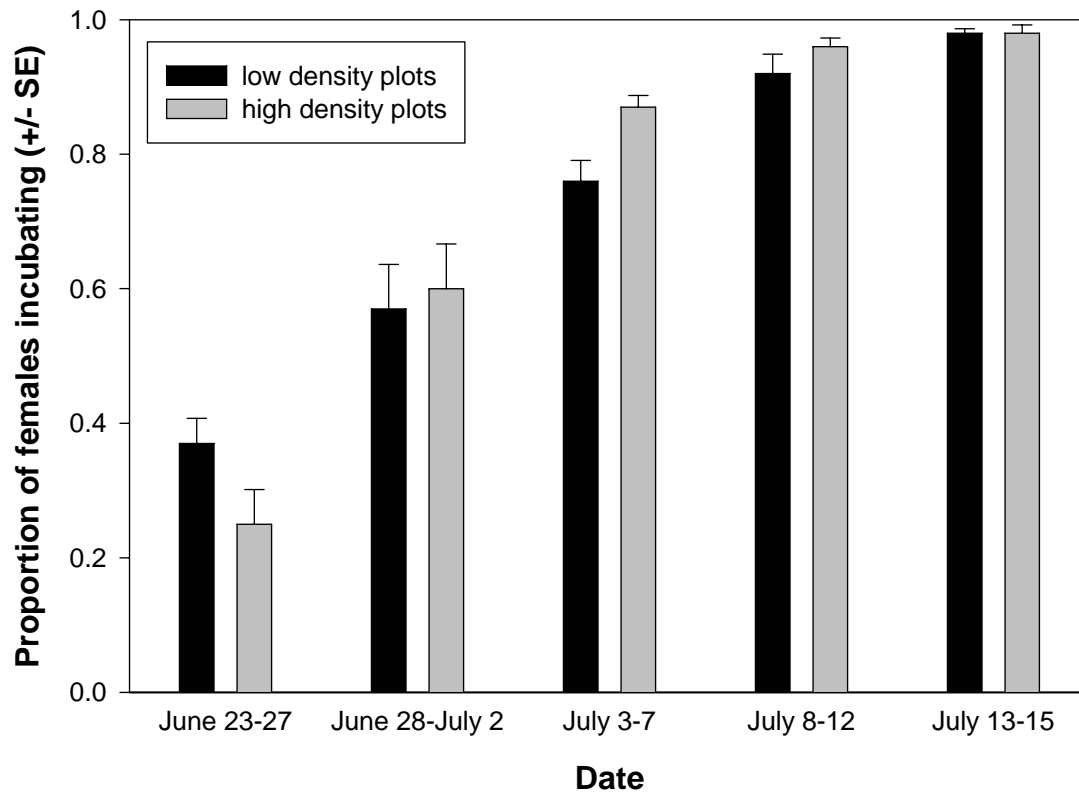


Figure 3.2. Proportion (mean \pm SE) of incubated common eider (*Somateria mollissima*) nests in low (≤ 8 nests established; 9 plots) and high (≥ 9 nests; 10 plots) density plots in relation to date in 2003. Frequency distributions of between groups were not different (K-S Test, two sample: $D_{MAX} = 0.039$, $n_{low} = 650$, $n_{high} = 2710$, $P = 0.403$). Data collected on Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada.

differ between high and low density plots.

3.4.1 Egg Concealment During Laying

Control nests, which contained little nesting material before laying, and treatment bowls with all nesting material removed had similar mean incubation onset dates (Figure 3.1). Mean incubation onset differed between bowls containing down and unmanipulated ones; nests were successfully initiated earlier in nest bowls containing down; this result maybe due to locational differences between the experimental nests and unmanipulated nests (experimental nests located nearer geographic centre of the colony; see below). However, I found a similar result when comparing only experimentally manipulated bowls. Bowls with down had nests successfully initiated in them earlier than bowls containing no nesting material, likely because they either survived better to the incubation stage (i.e., through egg laying), or were preferentially selected by early-laying females, or both. Down may provide better egg concealment than moss, and/or it may be preferentially used by early nesting females because it may indicate to laying hens that a bowl was used successfully in a previous year. Nest bowls with down may also be selected because of insulative benefits to females and their eggs. Moss-treated bowls appeared to have an intermediate incubation onset relative to other treatments, and larger sample sizes would likely aid in resolving possible differences between groups.

3.4.2 Colony-Wide Settlement Patterns

In 2003, nests were established earlier in some regions of the colony than others; plots nearer the geographic centre of the colony were occupied first, whereas plots nearer the main pond were filled later. Distance to ocean had no observable effect on timing of nesting. Higher quality females may have nested earlier at the colony interior (Coulson 1968; see also

Discussion Chapter 2), but I was unable to test this. Main pond was evaluated because it is used by a large number of eiders for landing, swimming, occasional copulations, the margin of the pond serves as a loafing area, and it appears to facilitate eider take-off and landing (see Schmutz et al. 1983, Robertson 1995). Perhaps few nests were established near main pond during early laying due to disturbances associated with high use by all species including gulls and geese, both known predators of eider eggs (Allard and Gilchrist 2002). Because my methods cannot account for nest abandonment or predation, my results would be confounded if higher nest loss occurred during egg laying in certain geographic regions. For example, peripheral regions of the colony may be more accessible to ‘floater’ herring gulls without established territories possibly resulting in higher predation rates.

No differences in timing of nesting between high and low density plots were observed (Fig 3.2). Although density is often used as a surrogate for habitat quality, this may be an incorrect assumption even among colony-nesting birds (Van Horne 1983). Nest density increased farther from the ocean. Again, this may be due to differences in predation risk, but no differences in relative egg capture rates (number of individual eggs captured by gulls per 180 minutes per 100 nests) between plots of different densities were detected at the colony in 2000 and 2001 (K. Allard pers. comm.). Unfortunately, I was only able to analyze nests in which laying was complete and incubation had commenced. Thus, further work is needed to address this problem.

3.5 Conclusions

Based on observations of eider females pushing loose materials (incl. moss, small rocks, vegetation, soil) into nest bowls during egg laying and my experimental results, I

conclude extraneous nest materials play a role in timing of eider nest establishment.

Experimental results showed that bowls containing down were more likely to have nests successfully initiated in them earlier than empty bowls, but I am unsure whether this was due to increased nest survival during laying, preference for bowls with down, or a combination of these factors.

Nest density did not vary strongly in relation to habitat variables measured, although density appeared to increase with increasing distance from ocean. Higher quality individuals may have nested earlier nearest the colony center (Coulson 1968), but no differences in timing of nest initiation were observed between high and low density regions. This is consistent with the finding that relative egg capture rates by gulls do not vary with different eider nesting densities at the colony (K. Allard pers. comm.), and suggestive that higher density regions may not have higher quality individuals.

CHAPTER 4: SYNTHESIS

4.1 Introduction

A basic assumption underlying habitat use studies is that increased fitness within certain habitats leads to increased use, producing non-random distribution patterns (Martin 1998, Clark and Shutler 1999). Non-random patterns of habitat use are often cited as evidence of causal selective processes, but proximate mechanisms underlying relationships between habitat use and natural selection are not fully understood. In other words, although numerous studies have evaluated whether habitat selection *patterns* are consistent with forces presumed to be selective (e.g., nest loss: Martin 1998, Brua 1999, Clark and Shutler 1999, Misenhelter and Rotenberry 2000), ecologists lack a comprehensive understanding of how the *process* of selection causes subsequent adaptation of habitat preferences and leads to non-random patterns of habitat use that they observe. Results of this study suggest that eider nest choices may reflect selective pressures involving the local predator community, egg concealment, nest microclimate and energy use, but mechanisms through which these preferences arose remain unclear. Although this discussion focuses primarily on nest site selection in birds, it could be extended further to avian habitat selection in general.

For evolution by natural selection to occur, there must be variation in a trait or attribute among individuals, a relationship between that trait and fitness, and inheritance of the trait (see Endler 1986 for further discussion). Clark and Shutler (1999) suggest natural selection could result in nest site and other habitat preferences that are genetic, imprinted, or learned. For this discussion, I will use Beltman and Metz's (2005) distinction between (4.2) "genetic habitat preference" and (4.3) "learned habitat preference," the latter of which I will further divide into preferences shaped by learning through (4.3.1) "imprinting" or "natal

habitat preference induction” (NHPI; Davis and Stamps 2004) (4.3.2) individual experiences or “personal information” (4.3.3) experiences of others or “social information” (Danchin et al. 2004). Natural selection could act to produce non-random distribution patterns through these proximate mechanisms either singly or in concert. In organisms for which habitat use preferences have direct genetic bases, differential fitness between individuals in different habitats should lead to changes in frequencies of alleles responsible for habitat choices (Beltman and Metz 2005). In contrast, natural selection may act through “learned habitat preferences” by means of increased fitness among individuals that learn adaptive strategies, provided learning traits are heritable (Figure 4.1; note that learning ultimately has a genetic basis).

4.2 Genetic/Innate Habitat Preferences

There is some evidence that habitat choices by arthropods and mollusks have genetic bases (Jaenike and Holt 1991), but bases of avian habitat selection are poorly understood (Martin 1988b, Clark and Shutler 1999). Cross-fostering experiments would aid in understanding processes underlying avian habitat choices (Davis and Stamps 2004). For example, they would help researchers determine if offspring choose nest sites/breeding habitats similar to those in which they were produced (i.e., prior to cross-fostering), or in which they were fostered.

When habitat choices are innate, maintenance of genetic variation could have evolutionary importance; Jaenike and Holt (1991) discuss the evolution of habitat preferences and explore adaptive mechanisms through which genetic variation for habitat preference

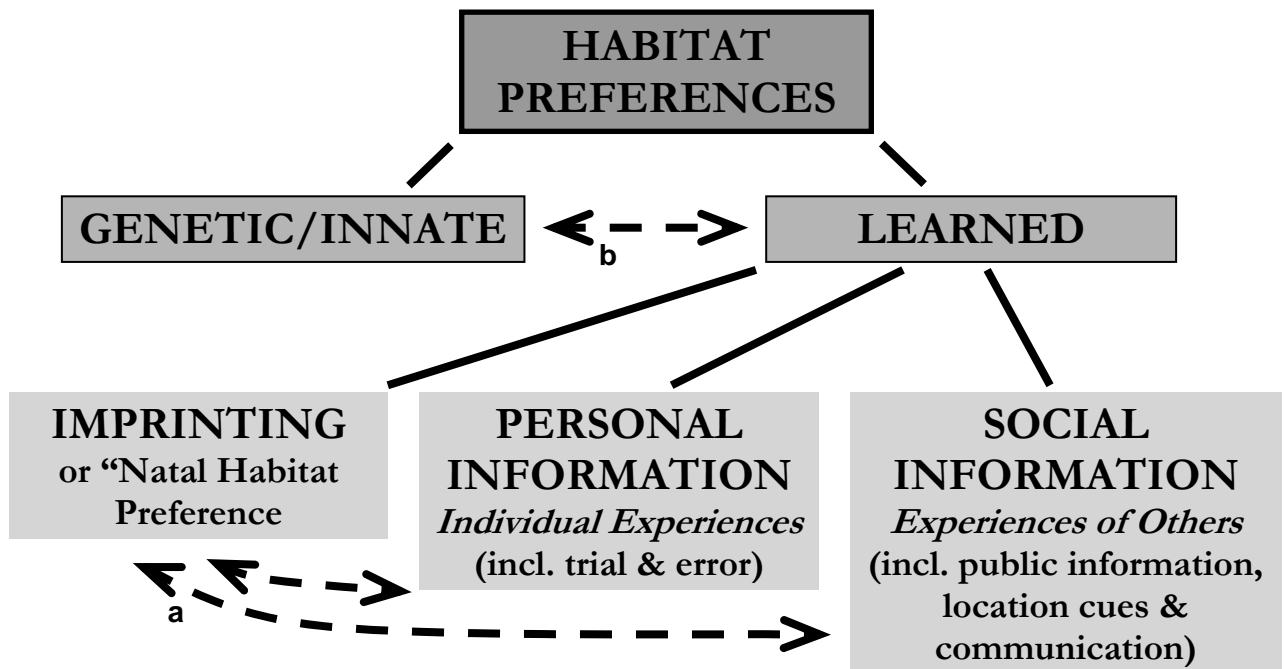


Figure 4.1 Habitat preferences can be shaped by information acquired genetically and through learning (nongenetically acquired information). Learned information is personal if it is acquired through individual experiences, or social if acquired vicariously (see Danchin *et al.* 2004). A special case of learning is information gained through imprinting, which may include both personal and social information^a. Note that learning ultimately has a genetic basis^b.

could be maintained. In general, habitat choices may reflect long-term optima (Clark and Shutler 1999) but individual differences in traits may make certain individuals more suitable to different niches (Davis and Stamps 2004), high quality habitats may be limited, and individuals may be relegated to suboptimal habitats. Furthermore, it is likely that switching strategies may also have adaptive benefits (Martin 1988a), which may further explain some of the variability in nest site choices I documented.

4.3 Learned Habitat Preferences

Learned habitat preferences may be proximate behavioural mechanisms through which natural selection can act to produce non-random distribution patterns (Beltman and Metz 2005). Even in the absence of inheritance, learning habitat preferences could lead to non-random habitat use patterns but this would not be reflective of true natural selection. The role of learning in nest building was highlighted by Scott (1902), who found hand-reared American robins (*Turdus migratorius*) capable of laying eggs were unsuccessful at building nests when presented with appropriate materials; in contrast, many species reared in novel habitats are capable of building species-characteristic nests (Sargent 1965).

4.3.1 Imprinting or Natal Habitat Preference Induction

Davis and Stamps (2004) argued that a unified understanding of natal experience effects on habitat preferences has been hampered in part by inconsistent terminologies across disciplines; although the term “imprinting” is most common in the vertebrate literature, they recommend “natal habitat preference induction” as a more inclusive term. NHPI is a potentially important source of individual variation in habitat selection, and the phenomenon has been observed in several avian species (Davis and Stamps 2004). Sargent (1965) found that natal experiences of zebra finches (*Taeniopygia guttata*) influenced nest building in some

circumstances, but not in others. Cross-fostered European cuckoos (*Cuculus canorus*; Teuschl et al. 1998) and village indigobirds (*Vidua chalybeata*; Payne et al. 2000), both brood parasites, spent more time in habitats in which they were reared than either habitats from which they were taken or novel habitats, and were more likely to lay in nests of species they were raised in. Natal experience may also influence preference for perching (Klopfer 1963), feeding (Greenberg 1984), and breeding (Tonniss et al. 2005) habitats. NHPI provides a mechanism by which individuals are more likely to select habitats to which they are suited, and has been shown to be an important source of individual variation in avian habitat selection (review in Davis and Stamps 2004). Although NHPI could be considered personal information, this information is gained in a unique context and may also include induction of social information.

4.3.2 Individual Experiences or “Personal Information”

Experience may also inform habitat use preferences. Danchin et al. (2004) distinguished between two types of experience, “personal information” and “social information.” Numerous studies have investigated the influence of prior experience on avian breeding dispersal (Greenwood and Harvey 1982, Drake 2006); increased likelihood and distance of breeding dispersal in response to negative experience would provide evidence that individual experience can influence subsequent habitat choices. Nest failure has been shown to increase likelihood and distances of breeding dispersal both within (see Jackson et al. 1989) and between (Clark and Shutler 1999, Powell and Frasch 2000, Winkler et al. 2004) seasons, although not in all studies (Shutler and Clark 2003, Fisher 2005). Experience with predators also can influence subsequent choice of nest cover type and quantity (Wiebe and Martin 1998). There may be advantages to site familiarity (Davis and Stamps 2004), which may

explain why some birds remain faithful to breeding sites despite being unsuccessful. This may be especially true among colonial nesters such as eiders that nest near kin (McKinnon et al. 2006), and are prone to catastrophic but random nest mortality events (e.g., polar bear predation). Furthermore, probability and distance of dispersal are likely influenced by both genetic and environmental factors (Weisser 2001, Pasinelli et al. 2004), and other factors including mate switching, nest ectoparasites and fluctuating food sources may also play important roles in dispersal (Fisher 2005).

4.3.3 Experiences of Others or “Social Information”

Animals may also base choices on what they have learned through the experiences of others. This is known as social information, which may include public information about resource quality (Danchin et al. 2004, Bednekoff 2005, see also Dall 2005, Danchin et al. 2005, Laland et al. 2005, Lotem and Winkler 2005). Little attention has been given to social information and its possible role in shaping habitat choices by birds, but recent information suggests it may inform breeding site choices in some species (Danchin et al. 1998, Doligez et al. 2002, Danchin et al. 2004, Ward 2005).

4.4 Conclusions

Despite demonstrating non-random nest site choice patterns amongst eiders, the extent to which eiders may use genetic or learned information to inform habitat choices is unknown. Several studies have highlighted the importance of evaluating habitat use *patterns* in the context of *processes* shaping habitat choices (Martin 1998, Clark and Shutler 1999, Misenhelter and Rotenberry 2000, Jones 2001, Davis 2005), but our understanding of proximate linkages between process and pattern remains inadequate. The role of learning in

habitat selection may have been underappreciated previously, but numerous studies have shown that both learned and genetic mechanisms may shape habitat preferences (although even learned preferences ultimately have genetic bases). Beltman and Metz (2005) suggest habitat selection could evolve through a genetic mechanism or by means of learning. Using theoretical models, they demonstrated that learned habitat preferences are likely to be characteristic of generalist populations, wherein they predict increased likelihood of disruptive selection and speciation. However, different costs of learning would have different implications for evolution and speciation with each mechanism (Beltman and Metz 2005). Eiders may adapt habitat choices based on learned information, but inheritance of traits is necessary to complete the criteria for natural selection (Endler 1986), and little is known about how habitat preferences are passed on.

In addition to further developing modern natural selection theory, understanding mechanisms underlying distribution of organisms among habitats would have great practical value when evaluating potential for adaptive evolution of habitat selection traits in response to anthropogenic and climate-driven habitat changes. Phenotypic plasticity can allow individuals to respond to short-term environmental changes, but microevolution (changes in gene frequencies between generations) through natural selection allows population adaptation to long-term changes (see Berteaux et al. 2004). In changing environments, selection could act to favor individuals better able to learn which habitats increase fitness and/or those with genetic/innate predisposition (i.e., alleles responsible for habitat preferences) to choose certain habitats where fitness is enhanced. Rate of habitat change and adaptive significance of different habitat selection strategies would likely have different implications for r- versus k-selected species (see Berteaux et al. 2004). If environmental conditions change, information

inherited genetically may not be useful (Danchin et al. 2004). In addition, reliance on genetic information when choosing habitat could lead to ecological traps (see review in Schlaepfer et al. 2002). Unfortunately, very little is known about mechanisms underlying habitat choice or the strength of phenotypic selection on behavioural traits (Kingsolver et al. 2001, see also Berteaux et al. 2004).

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**APPENDIX: EXPERIMENTAL EVALUATION OF NEST SHELTER EFFECTS ON
WEIGHT LOSS IN INCUBATING COMMON EIDERS *Somateria mollissima***

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ABSTRACT

Evaluating consequences of habitat selection is an important step in understanding life history strategies and behavioural decisions of animals. Kilpi and Lindström (1997) found that incubating common eiders *Somateria mollissima* on exposed, treeless islands lost weight faster than females nesting on wooded islands and proposed that this difference was due to adverse incubation conditions at exposed nests. Therefore, we tested whether common eiders gained an advantage when nesting in sheltered habitats by placing artificial shelters over randomly-selected females after the onset of incubation within an eider colony in arctic Canada. We predicted that sheltered females would be heavier on completion of incubation than control hens lacking shelters. Females nesting in artificial shelters experienced a more moderate thermal environment at both cold and warm temperature extremes. Eiders nesting in shelters were heavier than control females during late incubation, consistent with habitat-specific rates of weight loss reported by Kilpi and Lindström. Natural overhead cover was available at potential nests but few eiders used those sites. We suspect that microclimatic advantages offered by sheltered sites may be offset by costs of increased female vulnerability to predators. Further work is needed to test this hypothesis, and to determine mechanisms responsible for lower weight loss in eiders attending well concealed nests.

Introduction

Natural selection should favor habitat choices that maximize fitness. For example, nest site selection by oviparous animals likely reflects trade-offs between egg loss to predators, egg temperature maintenance (and thus egg viability), energetic costs to nest incubators, and adult survival. Nest predation, egg microclimate, embryonic development, and energetic costs of incubation have been well studied in birds (Williams 1996, Deeming 2002), but little is known about the energetic consequences of variation in nest microclimate among wild birds (Gloutney and Clark 1997). It has been presumed that many birds select nest sites to minimize energy expenditure, and limited evidence from several avian taxa suggests that protection of both embryos and nesting adults from heat stress may influence nest site placement and orientation (Hardy and Morrison 2001, Hoekman et al. 2002, Kim and Monaghan 2005). Energy expenditure increases above or below a homeotherm's thermal neutral zone, and birds are expected to choose nest sites within this zone to reduce thermoregulatory energy expenditure, thus leaving more energy for body maintenance and incubation.

The common eider *Somateria mollissima* is an appropriate species to study energetic consequences of nest site microclimate. Degree of shelter at nest sites varies considerably depending on local substrate and vegetation, and females may be exposed to wind, precipitation, and varying amounts of solar radiation. Furthermore, only females incubate (Goudie et al. 2000), typically females do not feed while incubating (Parker and Holm 1990, Bottitta 2001) and incubation constancy is among the highest observed among waterfowl species (reviewed in Afton and Paulus 1992, see also Bottitta 2001, Criscuolo et al. 2002,

Bolduc and Guillemette 2003a). Therefore, it is possible to study common eider incubation without having to account for off-nest energy expenditure and feeding.

Females undergo degenerative physiological and anatomical changes and may lose up to 45% of their total pre-incubation body weight (Cantin et al. 1974, Korschgen 1977, Parker and Holm 1990) during 24-26 days of incubation (Goudie et al. 2000). Kilpi and Lindström (1997) found that common eiders nesting on sparsely-vegetated, wind-exposed islands lost weight faster than did females nesting on wooded islands, and hypothesized that eider hens gained an energetic advantage by nesting in sheltered habitats. Therefore, we evaluated the importance of nest shelter on incubation weight loss by experimentally manipulating nest site characteristics. We set out artificial shelters on a random sample of eider nests in a treeless environment just after onset of incubation. Nest shelters provided overhead concealment and protection on two sides of the nest (east and west in all cases). Temperatures beside nest bowls in shelters and beside adjacent control nests were monitored using data loggers. We expected that shelters would ameliorate both hot and cold temperature extremes at the nest, and predicted that females nesting in shelters would be heavier than those without shelters near the end of incubation. We also predicted that eiders would choose nest sites based in part on local microclimate characteristics by selecting nest sites adjacent to, or beneath natural rock shelter.

Methods

Field Site

Work was conducted on Mitivik Island (64°02'N, 81°47'W) in the East Bay Migratory Bird Sanctuary, Nunavut, Canada in 2001 and 2003. The small (~800x400 m), low-lying (< 8 m elevation) island lies just south of the Arctic Circle, experiences almost continuous daylight

during the nesting season, and consists of granite rock interspersed with small patches of tundra, and several small ponds (< 0.5 ha). This island supports the largest known nesting colony of common eiders in the Canadian Arctic (up to 4000 pairs annually; Abraham and Ankney 1986).

Nest Shelter Experiment

Common eiders are known to nest under human-made shelters, and this method has been used to increase eider nesting density (Clark 1968, Jonsson 2001). In 2003, we used plywood nest shelters to provide individual nests with protection and shade. Shelters consisted of a 46 by 46 cm roof (with 12, 2.5 cm diameter holes to facilitate air flow), 25 cm high with 46 cm wide east and west facing walls (Figure A.1). In all cases, shelters were entirely open to the north and south.

Four regions of the island were used for study, each containing 30, 30, 28, and 12 nests under observation. Sheltered and control nests were randomly assigned in pairs, generally <10 m apart, so that they experienced similar sun exposure, temperature, humidity, and local nest density. Nests containing eggs with similar initiation date and incubation stage (number of days after onset of incubation) were alternately assigned as treatment or control (1st pair: control-shelter; 2nd pair: shelter-control, and so on). During shelter placement, we recorded clutch size and candled eggs to estimate incubation stage (Weller 1956). Nests too early or late in incubation and those with nearby rocks that prevented shelter placement were excluded as either shelter or control nests.

We were unable to obtain individual body weight at time of shelter placement because females trapped in early incubation frequently abandoned their nests in our preliminary trials,

Figure A.1. An example of a common eider *Somateria mollissima* nest protected with a plywood shelter. Shelters were placed over nests during early incubation on Mitivik Island, Nunavut, Canada, 2003.



as has been reported previously (Criscuolo 2001, Bolduc and Guillemette 2003b). Therefore, we obtained weights and body measurements of eiders captured 10-15 days after shelter placement. Shelters were placed and control nests assigned on 7-8 July, 2003. Plots were revisited once within 2-4 days of shelter placement. Shelters from abandoned nests were placed on other nests that 1) were nearest to those abandoned, 2) met previous criteria, and 3) were slightly later in incubation (at ~10 days of incubation). Nests were not revisited until females were captured. Analyses exclude nests abandoned due to shelter placement except where stated.

Nest Temperatures

We placed waterproof “Stowaway TidbiT® Temperature Loggers” (Onset Computer Corporation) immediately beside nests and recorded temperature at 15 minute intervals. TidbiTs® were attached using plastic cable ties to 7.6 cm screws and anchored into the ground at the south edge of nest bowls during shelter placement. Loggers were positioned to ensure they would not be covered by nest down or incubating females, and were in contact with the rim of the nest bowl to allow for conduction (see Shine and Kearney 2001, Dzialowski 2005).

Naturally-Occurring Nest Shelter

Common eiders nest on the ground; typically in shallow depressions which they line with down feathers (hereafter, ‘nest bowls’). In the Canadian Arctic, most nests are established in pre-existing nest bowls, while a few females construct their own (e.g., on sand beaches). In many northern locations, nest bowls are well established and could reflect hundreds of years

of occupation (Cooch 1965, Jonsson 2001). Existing nest bowls at this colony are re-used in different years and are easily identified prior to arrival by nesting females.

Following hatch in 2001, physical characteristics were recorded for all nest bowls present within five long-term study plots (bowls used by nesting eiders $n = 404$; unused $n = 385$) and at non-nest sites ($n = 217$) sampled systematically (Krebs 1999) in plots at 10 meter grid intervals. Due to lack of tall vegetation (none > 8 cm), rocks provided the only direct overhead cover for nesting eiders at this colony. Consequently, we recorded whether overhanging rocks provided direct overhead shelter at each site, and also the occurrence of rocks adjacent to nest bowls. To evaluate presence/absence of direct overhead nest cover, an observer stood directly over each nest bowl (from 1 meter above bowl) and recorded if a round plate (diameter 20 cm, centered in nest bowl) was partially obstructed by overhead rock. To document occurrence of rocks adjacent to nest bowls, one end of a meter-long stick was placed in the center of the nest bowl, oriented 45° above horizontal, and rotated through 360° . Rock structure was considered present if rock obstructed this rotation at any time. For example, rock was recorded as being present to the north if stick movement was obstructed by rock between 337.5° and 22.5° .

Statistical Methods

Principal components analysis (PCA) was used to develop an index of female structural size using tarsus (length of the tarsometatarsus bone only), flattened wing, and total head-bill (length from the occipital ridge to the tip of the bill) lengths. The first component accounted for 62% of the total original variance and described positive covariation among tarsus, wing, and head lengths (loadings of 0.53, 0.57, and 0.63, respectively). We captured 65 birds (34

sheltered, 31 control). Single morphological measurements were missing from two birds, so these measurements were estimated using the regression relationship between PC1 scores and body measurements. Morphological measurements were missing entirely for two birds.

Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to select models that best fit the data (Akaike 1985, Burnham and Anderson 2002). Analysis of Covariance (ANCOVA, SAS PROC GLM, SAS Institute 1990) evaluated differences in female weight between treatments (group variable) while simultaneously controlling for effects of incubation stage and body size (covariates). All 2-way interaction terms were included when developing the candidate model set. Unbiased estimates of mean weight of control and sheltered females are given as least squares means \pm SE (LSMEANS, SAS Institute 1990).

Differences in daily maximum, minimum, and mean nest site temperatures between control and sheltered nests were evaluated using repeated measures Multivariate Analysis of Variance (MANOVA; SAS PROC GLM). Treatment was the explanatory variable of interest, day was the repeated factor for each nest, and maximum, minimum, and mean daily temperatures were response variables. An initial model considered effects due to treatment, day, and treatment*day interaction.

Fisher's exact test was used to compare differences in frequency of nest bowls having direct overhead cover from rocks at all nest bowls (occupied and unoccupied combined) versus non-nest sites. In addition, differences in frequency and orientation of rock structure adjacent to nest bowls were evaluated using G-tests and Raleigh's test for circular uniformity.

Results

Nest Shelter Experiment

Nests were observed 2-4 days after initial shelter placement; 25 hens with shelters abandoned their nests. Clutch size of sheltered birds did not differ between those that abandoned and those that did not (G-test, $G_1 = 5.08$, $df = 5$, $P = 0.41$) but, as expected, abandonment may have been more likely to occur at nests disturbed earlier in incubation (Days incubating 5.8 ± 3.5 SD abandoned versus 7.4 ± 2.1 SD accepted; t-test, $t = 1.87$, $df = 48$, $P = 0.068$).

We captured 65 females (34 experimental, 31 control) in mid to late incubation. Body weight was weakly related to size index ($r^2 = 0.136$, $n = 61$, $P = 0.004$). There were no differences in structural measures between treatment or control groups (tarsus, wing length, head-bill; t-tests, all $P_s > 0.7$). There were also no differences in clutch size between treatment and control groups, either upon shelter placement or at capture (G-tests, $P_s > 0.37$). Incubation stage at time of shelter placement was approximately 2.5 days earlier for controls (7.2 ± 3.3 SD control versus 9.6 ± 2.6 SD sheltered; t-test, $t = 3.34$, $df = 63$, $P = 0.001$). Estimated nest initiation date was marginally advanced for sheltered hens (175.4 ± 3.3 SD sheltered versus 176.6 ± 3.5 SD control; t-test, $t = 1.76$, $df = 63$, $P = 0.084$). Incubation stage did not differ between controls and sheltered nests at capture (21.7 ± 1.5 SD versus 21.7 ± 1.5 SD, respectively; t-test, $t = 0.17$, $df = 63$, $P = 0.87$).

Fifteen candidate models were developed to assess the importance of sheltering nest sites (Treatment), Incubation Stage (Stage), and Body Size in explaining late incubation body weight. The top five models ($\Delta AIC_c \leq 4$) all included Treatment (i.e., shelter), Stage, and Body Size (Table A.1). Two of 5 also included the Stage*Treatment interaction, and 3 of 5 included Stage*Body Size interaction.

Table A.1. Ranking of models assessing the importance of sheltering nest sites (Treatment), incubation stage (Stage), and body size in explaining late-incubation body weight of common eider females captured on Mitivik Island, Nunavut, Canada, 2003. Models are ranked using Akaike's Information Criterion adjusted for sample size (AIC_c). RSS = Residual Sum of Squares, n = number of females measured, K = number of parameters, ΔAIC_c = difference in AIC_c between model and the one with minimum AIC_c , Weight = Akaike weight.

Model ^a	RSS	n	K	AIC_c	ΔAIC_c	Weight
Treatment, Stage, Body Size, Stage*Body Size, Stage*Treatment	389524	63	7	581.35	0	0.368
Treatment, Stage, Body Size, Stage*Body Size	415702	63	6	583.07	1.71	0.156
Global ^b	384747	63	8	583.11	1.76	0.153
Treatment, Stage, Body Size, Stage*Treatment	420161	63	6	583.76	2.40	0.111
Treatment, Stage, Body Size	442051	63	5	584.63	3.27	0.072

^a includes only models $< 4 \Delta AIC_c$

^b includes Treatment, Stage, Body Size and all two-way interactions

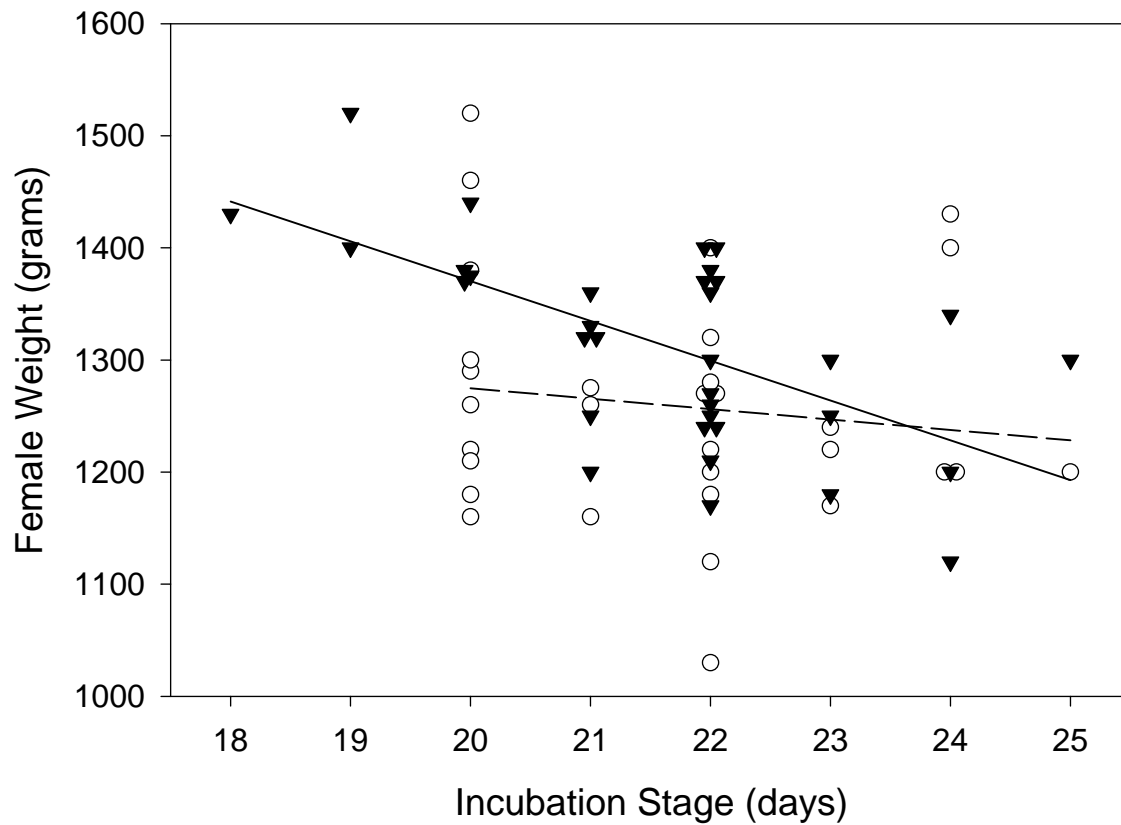
Based on these results, we conducted an analysis of covariance (ANCOVA) in which eider body weight was the dependent variable, treatment was a categorical variable, and body size and incubation stage were covariates (Treatment, Stage, Body Size, Stage*Treatment, Stage*Body Size). After controlling for covariate effects, females with shelters (Least squares mean 1312.4 ± 14.2 SE grams) were about 45g heavier than control females (1266.0 ± 15.4 SE grams) near the end of incubation ($P = 0.033$).

The relationship between incubation stage and weight differed between treatment and control females (ANCOVA interaction, $F_{1,57} = 3.83$, $P = 0.055$). Late incubation body weight declined with incubation stage among sheltered hens ($Y_t = 2082.5 (\pm 179.9 \text{ SE}) - 35.7 (\pm 8.3 \text{ SE})$, $r^2 = 0.35$, $n = 34$, $P < 0.001$). Control birds were lighter, but collectively their weights did not appear to decline as rapidly ($Y_c = 1460.5 (\pm 279.2 \text{ SE}) - 9.3 (\pm 12.8 \text{ SE})$, $r^2 = 0.02$, $n = 31$, $P = 0.48$) (Figure A.2). ANCOVA also indicated a significant interaction between Incubation Stage and Body Size (ANCOVA interaction, $F_{1,57} = 4.48$, $P = 0.039$). To explore this interaction we combined both treatment and control birds and classified individuals into “large” ($PC1 \geq 0$) and “small” ($PC1 < 0$) categories. Late incubation body weight declined among small females ($Y_{sm} = 1923.0 (\pm 215.3 \text{ SE}) - 30.4 (\pm 9.8 \text{ SE})$, $r^2 = 0.19$, $n = 37$, $P = 0.004$), but weights among large females did not show this trend ($Y_{lg} = 1531.4 (\pm 254.3 \text{ SE}) - 9.6 (\pm 11.6 \text{ SE})$, $r^2 = 0.01$, $n = 28$, $P = 0.43$).

Nest Temperatures

Temperature data were obtained for 10 sheltered and 10 control nests where we captured females. In 2 control nests and 1 sheltered nest, temperature loggers rarely (0.37% of observations) exceeded maximum recording temperature ($\sim 38^\circ\text{C}$) but when this occurred

Figure A.2. Stage-specific weights of 65 incubating female common eiders *Somateria mollissima* nesting in human-made plywood shelters placed between 4 and 15 days incubation (filled triangles, solid line; n = 34) and at adjacent, unmanipulated sites (open circles, dashed line; n = 31). Females were captured 10-15 days after shelter placement. Work was conducted on Mitivik Island, Nunavut, Canada in 2003.

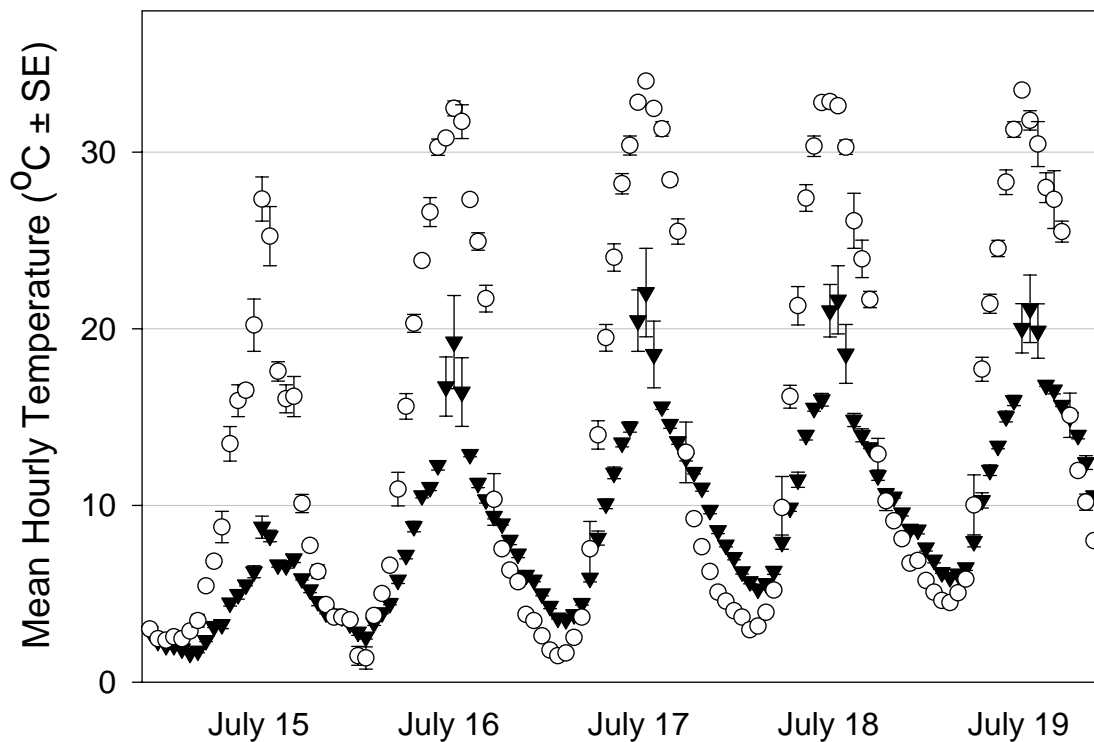


we used a value of 38°C. There was no interaction effect for maximum, minimum, and daily mean temperatures in our initial MANOVA model (all P s ≥ 0.16), so the interaction term was dropped from further analyses. Birds in sheltered nests experienced more moderate environmental temperatures compared to controls; daily maximum and mean temperatures were lower in sheltered nests ($F_{1,252} = 35.99$, $P < 0.0001$ and $F_{1,252} = 40.39$, $P < 0.0001$, respectively) and daily minimum temperatures were higher in sheltered nests ($F_{1,252} = 51.66$, $P < 0.0001$; see Figure A.3 for example). Mean daily maximum and mean temperatures of sheltered nests were cooler than controls by approximately 5.0°C (LS Means, 95% CI 3.3 to 6.6) and 2.3°C (LS Means, 95% CI 1.6 to 3.0), respectively. Mean daily minimum temperatures of sheltered nests were warmer than controls by approximately 1.1°C (LS Means, 95% CI 0.8 to 1.4).

Naturally-Occurring Nest Shelter

Although few sites of any type had naturally occurring overhead cover (5 of 217 non-nest sites; 4 of 787 nest bowls, occupied and unoccupied combined), non-nest sites were more likely than nest bowls to have overhead cover in 2001 (Fisher's exact test, 2-tailed, $P = 0.026$). Furthermore, few occupied (2 of 404) or unoccupied nest bowls (2 of 383) had overhead rock cover. However, eiders preferentially selected nest sites near rocks. Nest bowls (used and unused combined) were more likely to be situated adjacent to rocks (≥ 1 nearby rock detected) than non-nest sites ($n = 787$ and 217 , respectively; G-test, $G_1 = 27.54$, $df = 1$, $P < 0.001$). Further, 42.6% of nest bowls (335 of 787; used and unused combined) had nearby adjacent rocks, compared to 23.5% (51 of 217) of non-nest sites. Active nests were also more likely to have nearby rocks when compared with unused bowls ($n = 404$ and 383 ,

Figure A.3. Mean hourly nest temperatures ($^{\circ}\text{C} \pm \text{SE}$; recorded at nest bowl edges July 15-19, 2003) at two adjacent common eider *Somateria mollissima* nests (8.5 m apart) on Mitivik Island. Unsheltered control hen (open circles) experienced higher daily maximum and mean temperatures, and lower daily minimum temperatures when compared to hen nesting under human-made plywood shelters (filled triangles). This general pattern was observed experiment-wide (see results).



respectively; G-test, $G_1 = 5.28$, $df = 1$, $P = 0.021$). Specifically, 46.5% (188 of 404) of active nests had nearby adjacent rocks, compared to 38.6% (148 of 383) of unused nest bowls.

Although eiders were more likely to select nest sites adjacent to rocks, no directional preference was detected when comparing the orientation of rock structure adjacent to active nests versus unused nest bowls (i.e., direction of nearby rocks in relation to each nest bowl; G-test, $G_1 = 7.88$, $df = 7$, $P = 0.34$). Furthermore, the orientation of rock structure was uniformly distributed among active nest bowls having nearby rock (Raleigh's test for circular uniformity, $z_{0.05,500} = 2.302$, $P > 0.10$).

Discussion

Our experimental results are consistent with habitat-specific rates of weight loss in common eiders first reported by Kilpi and Lindström (1997). As predicted, eiders nesting under shelters maintained better body condition during mid incubation. The differences in weight we detected may be explained by the more moderate temperatures experienced by hens nesting under shelters. Similar to Kim and Monaghan's (2005) results, temperature data indicated that nest shelter moderated both hot and cold temperatures experienced by nesting females, often by 10°C or more (Figure A.3). Eiders under shelters may have lost weight at a faster rate during late incubation than lighter control hens. Perhaps control hens lost weight at faster rates earlier in incubation, and then responded to this by altering incubation behaviours which slowed their rate of weight loss later in incubation as has been observed among eiders previously (Bottitta 2001, Criscuolo et al. 2002).

Disturbance of eiders during early incubation is known to induce nest abandonment (Criscuolo 2001, Bolduc and Guillemette 2003b), consistent with our observation that

abandonment may have been more likely to occur at nests disturbed earlier in incubation. Consequently, we were unable to weigh birds prior to shelter placement and could not directly assess if abandonment of some sheltered birds was related to their body condition (Criscuolo 2001). In other words, the pattern we observed could have been produced if only the best quality females had remained following shelter placement. We presume abandonment occurred randomly and was not related to female quality for the following reasons. Evidence from other seabirds (Hipfner 1997, Morbey and Ydenberg 2000, Arnold et al. 2004) and anatids (Erikstad and Tveraa 1995, Dalhaug et al. 1996, Lepage et al. 2000) suggest that timing of breeding and clutch size is frequently related to parental quality, and that late-nesting birds are less successful than those that nest early. There was no detectable difference in clutch size between birds that abandoned and those that did not, and both groups made similar nest site choices (i.e., similar nesting regions, nest habitat, local macroclimate, and nesting densities). Moreover, had abandonment been more likely to occur in poor-condition birds, we would have expected to find differences in nest initiation date, clutch size, and body size between control and sheltered birds within our experiment (see Milne 1976, Erikstad and Tveraa 1995, Hanssen et al. 2002, Yoccoz et al. 2002, Hanssen et al. 2003a). However, we detected no differences between any of the groups (see results), and have no reason to suspect that female quality differed between control and sheltered hens, or among sheltered hens that abandoned and those that did not.

Nest Temperatures

Operative temperature (T_e) is a better measure of thermal environments experienced by birds, as it integrates convection (combined effect of air temperature and wind), radiation (solar and

thermal), and conduction (Bakken et al. 1985, see also Gloutney and Clark 1997).

Taxidermic mounts and animal models have been developed to estimate avian T_e (e.g. Fortin et al. 2000), but this approach would have been impractical at our remote field site. We are not aware of any studies that test the utility of TidbiT® Loggers in estimating avian T_e , but they produce sets of T_e nearly identical to models that mimic North American lizards (Vitt and Sartorius 1999).

Lower critical temperature of eiders from Svalbard was estimated in summer (Gabrielsen et al. 1991) and winter (Jenssen et al. 1989) at 7°C and 0°C, respectively. In our study, 46.2% of temperatures beneath shelters were below 7°C compared with 43.5% at control nests. Furthermore, 0.3% of temperatures recorded beneath shelters were below 0°C compared with 3.6% at control nests. Energy expenditure also increases at higher temperatures (Conway and Martin 2000). Jenssen et al. (1989) experimentally induced heat stress in 3 common eiders, and demonstrated that metabolic heat production increased drastically at 32°C. 1.8% of temperatures recorded beneath shelters were above 32°C compared with 3.2% at control nests. Eiders at our colony were frequently observed “panting” on warm days, and we suggest that heat stress and dehydration may also be energetically costly to eiders. Therefore, it is likely that eiders nesting under shelters gained an additional advantage by experiencing lower daily maximum temperatures. Furthermore, increased ambient temperatures lead to more rapid dehydration, presumably increasing frequency of incubation breaks which are known to put eggs at greater predation risk (see Bottitta 2001).

Late Incubation Body Weight

Fitness costs of reduced body condition during incubation may be significant; eiders in poor condition may have lower nest success (Bottitta et al. 2003, Hanssen et al. 2003b see also Erikstad and Tveraa 1995, Hanssen et al. 2003a), be more likely to abandon their ducklings in crèches to be guarded by other females (Bustnes et al. 2002, Hanssen et al. 2003c), and be less likely to breed in subsequent years (Yoccoz et al. 2002). Small differences in late incubation body weight have been shown to influence probability of nest abandonment in other waterfowl (Blums et al. 1997). Although Erikstad and Tveraa (1995) suggested that common eiders do not compensate for depletion of body reserves when mass reaches a critical point, recent evidence suggests that eiders are capable of modifying incubation behaviours to slow weight loss during late incubation (Criscuolo et al. 2001, Criscuolo et al. 2002, Bottitta et al. 2003). Typically, the daily rate of weight loss declines as common eider incubation progresses (Gabrielsen et al. 1991, Criscuolo et al. 2002) and, in late incubation, female eiders in poor condition may slow rate of weight loss by increasing water intake (Gabrielsen et al. 1991), recess frequency (Bottitta 2001), or sleep frequency and duration (Criscuolo et al. 2001). In our study, control eiders weighed less than sheltered birds but appeared to have lower rates of daily weight loss late in incubation (Figure A.2), suggesting that control females may have employed strategies including sleep changes or increased water consumption to maintain body weight late in incubation. Eiders in poor condition may also change incubation habits; eiders whose incubation was experimentally prolonged re-initiated feeding (Criscuolo et al. 2002), and increased frequency and duration of incubation recesses often to drink (Criscuolo et al. 2002, Bottitta et al. 2003). Consequently, females whose incubation was experimentally extended lost weight at a slower rate than during their normal

incubation period. Furthermore, manipulated females that were successful took fewer incubation breaks than unsuccessful ones, who likely lost their eggs to herring gulls *Larus argentatus* while away from the nest (Bottitta et al. 2003). In this study, unsheltered eiders in poor condition may also have increased frequency and/or duration of incubation recesses, or abandoned their nests (Korschgen 1977, Criscuolo et al. 2002).

Nest Concealment and Predator Community

Despite demonstrating that temperatures were more moderate under shelters and that naturally occurring sheltered nest sites were available on the study island, few eiders (< 1%) nested at sites with direct overhead shelter. Perhaps a trade-off exists for common eiders at this colony, in which sheltered sites offer microclimatic advantages to nesting eiders (Kilpi and Lindström 1997, Figure A.3) but increase risk of female mortality or egg loss because it could be more difficult to detect and monitor predators from beneath sheltered sites. Eiders are long-lived, and would be expected to sacrifice eggs or duckling care in order to prevent mortality and loss of future breeding opportunities in an effort to maximize lifetime reproductive success (Bustnes et al. 2002). We would therefore predict that eiders would choose against concealed nest sites if they increased risk of adult mortality by “trapping” females at nest sites. Nest cover has been shown to increase nest success in common eiders at breeding locations with few or no mammalian predators (Choate 1967, Milne and Reed 1974, Schmutz et al. 1983), but may decrease success on islands accessible to arctic fox (*Alopex lagopus*; Noel et al. 2005). Eiders nesting on islands with few mammalian predators in Maine and Nova Scotia also readily used artificial plastic and wooden nest shelters, which also increase nest success (Clark 1968, Woolaver 1997). In contrast, eiders appear to avoid nest sites with artificial and

natural overhead cover where mammals are common nest predators (see Laurila 1989, Divoky and Suydam 1995, Noel et al. 2005). We found eiders select sites with no direct overhead cover despite possible microclimatic (Kilpi and Lindström 1997, this paper) and concealment advantages (Choate 1967, Milne and Reed 1974, Noel et al 2005; but see Gerell 1985), suggesting that nest concealment may be costly to eiders and/or monitoring predator activity may be beneficial at this colony. Herring gulls were the primary nest predator (K. Allard, in prep.); although continued observer presence in recent summers appears to have deterred their visitation to the colony, Arctic fox and polar bears *Ursus maritimus* are also known to visit the study island and prey upon eiders and their nests (P. Fast, pers. obs). In contrast, Cooch (1965) reports common eiders nesting on nearby islands off southwest Baffin Island “selected sites surrounded by rock, or under an overhang, or, preferably, both” but doesn’t report mammalian predators on these islands. If costs of nesting in sheltered habitats are lowered due to absence of mammalian predators, trade-offs between thermoregulation, concealment from predators, and visibility (Götmark et al. 1995) would be altered and could influence site choice patterns. Our findings appear to reflect these trade-offs; eiders at our study site chose sites that provided some microclimatic advantages, but not to an extent where observation of their surroundings was compromised. Further investigation into the trade-offs between microclimate, energy use by incubating birds, and predation risk would add greatly to our understanding of habitat choice trade-offs. Furthermore, behavioural (e.g., nest attendance) and body composition data would aid in elucidating both our results and those of Kilpi and Lindström’s (1997).

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